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ABSTRACT

North and South Anatolia areas are today refuge areas for plants that were previously widespread in the European and Mediterranean regions. Thirteen well-dated Anatolian pollen records spanning the last 23 million years allow for a reconstruction of the history of several plants that have disappeared from this region or are surviving in this refuge area. For example, in this study we show that *Cedrus* is an ancient element of the Anatolian flora. Tropical elements lived in this area until the early Pliocene. Subtropical elements became extinct in the Middle to Late Pleistocene, except for *Glyptostrobus* (Taxodiaceae swamp tree) and *Carya* (Juglandaceae, a warm-temperate tree), which may have persisted until recently in this area. In addition, a comparison of palaeofloras coming from different locations ranging from 36–38°N and 40–42°N latitudinal intervals in the northeastern Mediterranean (including Anatolian coastal regions) with those from Europe and North Africa has been done. This shows that the North and South Anatolia areas appear to have been separate refuges for thermophilous-hygrophilous plants since the early Pliocene (*ca*. 5 Million years). Today, Anatolia is a plant refuge area for warm-temperate species, which have almost completely (*Zelkova*) or completely (*Pterocarya*, *Liquidambar*, *Parrotia persica*) disappeared from other European and peri-Mediterranean regions. Taxodiaceae swamp ecosystems (*Glyptostrobus*) might have recently disappeared from the southern Black Sea shoreline. New pollen data from Anatolia also allowed us in calibrating the timing of floristic extinctions at a continental scale and helped us in clarifying the reasons of the different floral extinctions and dynamics (breaking up and shifting) in the refuge areas. Thanks to global warming there is a potential for the survival and expansion of thermophilous species (*Pterocarya fraxinifolia*, *Zelkova abelica*, *Liquidambar orientalis*) in this area.

Keywords
Plant refuges, Pollen, late Cenozoic, Anatolia

Highlights
> Pollen records from Anatolia show succession of plant extinctions since 23 Ma. > North and South Anatolia are separated refuges for thermophilous/hygrophilous plants since 5 Ma. > *Glyptostrobus* swamps recently disappeared from the southern Black Sea shoreline. > *Cedrus* has been a continuous component of the Anatolian flora since at least 23 Ma.

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1. Introduction

Thermophilous and hygrophilous flora from southern Europe and the southern Mediterranean area (including the Near East) has suffered a lot of extinctions during the late Cenozoic. These extinctions have been documented by plant macrofossils (Follieri, 2010; Follieri et al., 1986; Kovar-Eder et al., 2006) and, for the most part, by pollen records (Suc et al., 1995b; Suc and Popescu, 2005; Jiménez-Moreno and Suc, 2007; Jiménez-Moreno et al., 2007; Leroy, 2007; Magri, 2010). Two major steps of extinction have been identified at 14 million years (Ma) and 3.4 Ma (Suc et al., 1999, 2004). The first step corresponds to a global decrease in temperature (Zachos et al., 2001), moderately recorded in the Mediterranean region (Fauquette *et al*., 2007), during which the most thermophilous plants disappeared from the northern coastlines (Jiménez-Moreno and Suc, 2007; Jiménez-Moreno et al., 2007), in a context already characterized by a strong latitudinal increase in dryness (Fauquette et al., 2007; Jiménez-Moreno and Suc, 2007). The second step corresponds to a minor global climatic cooling (Shackleton et al., 1995) that in the Mediterranean region was more characterized by an increase in dryness and enhanced seasonal contrast (Suc, 1984; Suc et al., 1995b; Popescu et al., 2010).

According to the plant classification by Nix (1982), five plant groups can be differentiated according to the mean annual temperature (MAT) under which they grow:

- megathermic (tropical): MAT>24°C;
- mega-mesothermic (subtropical): 20°C<MAT<24°C;
- mesothermic (warm-temperate): 14°C<MAT<20°C;
- meso-microthermic (cool-temperate): 12°C<MAT<14°C;
- microthermic (boreal): MAT<12°C.

Most of the megathermic taxa disappeared from the northern Mediterranean shorelines during the early Serravallian (14 Ma) and a large number of mega-mesothermic plants became extinct in this region at *ca*. 3.4 Ma (Suc et al., 1999, 2004). Since then, the remaining mega-mesothermic (Taxodiaceae, *Nyssa p.p.*), mesothermic elements (*Liquidambar*, *Pterocarya*, *Carya*, *Nyssa p.p.*, *Zelkova p.p.*) and meso-microthermic to microthermic elements (*Cathaya*, *Cedrus*, *Tsuga*), requiring high precipitation, persisted in some reduced areas during a certain time according to

latitude, altitude, differences in slope exposure and microclimate (Suc et al., 1995b; Suc and Popescu, 2005).

Taxa that disappeared from southern Europe belong to several families. For example: (1) megathermic plants: Leguminosae, Sapindaceae, Bombacaceae (*Bombax*), Verbenaceae (*Avicennia*), Euphorbiaceae (*Alchornea*, *Amanoa*), Sapotaceae; (2) mega-mesothermic plants: Hamamelidaceae (*Distylium*, *Hamamelis*, *Fothergilla*), Lauraceae, Juglandaceae (*Engelhardia*, *Platycarya*), Taxodiaceae, Arecaceae; (3) mesothermic plants: Hamamelidaceae (*Liquidambar*, *Parrotia*), Juglandaceae (*Carya*, *Pterocarya*); (4) meso-microthermic plants: *Cathaya* (coniferous today restricted to China; Wang, 1961) and (5) microthermic plants: *Tsuga* and *Cedrus*. Timing and causes of these extinctions are generally explained by successive coolings in the northern hemisphere and Mediterranean aridification since *ca*. 14 Ma. This resulted in two present-day refuge areas on longitudinal fringes in the Mediterranean (Suc et al., 2004). For example, *Zelkova*, *Pterocarya* and *Liquidambar* remained in the northeastern Mediterranean region. *Laurus* and *Argania* (Sapotaceae) remained in the southwestern Mediterranean region. *Cedrus* persisted in both regions (Quézel and Médail, 2003). *Pterocarya fraxinifolia* and *Liquidambar orientalis* are the only thermophilous trees that persisted in Anatolia (coastlines and nearby slopes). Anatolia then appears as the most important refuge area (Zohary, 1973; Quézel and Médail, 2003) as shown by its high plant diversity (Médail and Diadema, 2009).

In this study we address the following questions: is the refuge status of Anatolia recent or was acquired in the past? Was this area subject to successive floral extinctions since the past 14 Ma due to climatic change? Otherwise, is Anatolia characterized by the same floral history as other Mediterranean regions? Pollen can help us in answering these questions. However, in this region, pollen studies were traditionally performed without a robust botanical background and as such have been poorly useful in this way (Nakoman, 1967; Benda, 1971; Akgün and Akyol, 1999). Since the 2000's, we have been performing an intensive effort in the botanical identification of late Cenozoic pollen grains from Anatolia, allowing for more detailed information about vegetation changes. In this synthesis, we compare new pollen records (Fig. 1a) from twelve sites (discontinuous documentation of the Miocene and early Pliocene) and a long core, DSDP Site 380 (continuous record of the last 6 Ma from southwestern Black Sea), with pre-existing pollen data from Europe and North Africa.

2. Current vegetation and flora of Anatolia

2.1. Vegetation

Present-day vegetation of Anatolia is complex and relates to the Mediterranean, Irano-Touranian, European and Euxino-Hyrcanian phytogeographic regions (Fig. 1c; Denk, 1998).

The West and South coastal areas are characterized by the Mediterranean realm, which also sporadically characterizes the North shoreline and some encased valleys within the Pontic Ranges. Several bioclimates and altitudinal vegetation belts have been defined according to rainfall and altitude (Quézel and Médail, 2003): a thermo-Mediterranean belt with *Olea europea* and *Pistacia lentiscus* where *Ceratonia* is scarce; some riparian forests with *Liquidambar orientalis* and *Platanus orientalis*; a meso-Mediterranean belt characterized by sclerophyllous oaks, where *Quercus ilex* is very rare; a supra-Mediterranean belt inhabited by deciduous associations including *Carpinus orientalis* and *Ostrya carpinifolia*; a Mediterranean montane belt composed of altitudinal conifers with *Cedrus libani* occupying significant areas on the Taurus and Anti-Taurus massifs and an oro-Mediterranean belt characterized by meadows and steppes.

The Irano-Touranian region, encompassing the Anatolian Plateau, is affected by annual precipitations lower than 200 mm. A diversified steppe vegetation, where *Artemisia* is relatively subsidiary, occurs in this area (at least to the West). Pre-steppic structures less subject to human impact with trees (*Pinus pallasiana* and *Juniperus excelsa* westward, *Quercus libani*, *Q. brantii* eastward) only appear on reliefs where precipitations are higher.

The European region is secondary in Anatolia, and is only represented by some deciduous hilly stands with *Quercus* and *Carpinus betulus*.

The Euxino-Hyrcanian region, characterized by high precipitations and the lack of summer drought, develops along the Black Sea shoreline. There, wonderful hilly forests still exist, dominated by deciduous elements (mostly *Quercus hartwissiana*, *Q. macranthera*, *Carpinus betulus*, *Castanea sativa*, *Fagus orientalis*, *Rhodendrum ponticum*, *Rh. flavum*). Riparian forests also occur, with *Alnus, Fraxinus*, and *Pterocarya*. The montane belt is mainly occupied by *Fagus orientalis* and *Rhododendron ponticum*, with occurrences of *Abies nordmanniana,* and *Picea orientalis* restricted to the East. The subalpine and alpine belts are mainly developed to the East where influence of Caucasus relief prevails within a diversified flora (*Juniperus communis* and *J. sabina* coexist with several Ericaceae).

2.2. Anatolia: present-day plant refuge area

Anatolia is today a refuge area of Neogene and early Pleistocene Mediterranean flora. Some mesothermic Eurasian taxa such as *Liquidambar*, *Parrotia*, *Pterocarya*, *Zelkova* and *Cedrus* (microthermic tree) persisted through the European Neogene and can still be found in reduced areas in the Anatolian landscape and in the Hyrcanian zone (Quézel and Médail, 2003). *Zelkova crenata* occurs today in two very restricted riparian localities in easternmost Anatolia, close to the Van Lake, although it is still well developed in Abkhazia, Small Caucasus, and mainly in the Hyrcanian region (Zohary, 1973). In addition, this genus is still present in very restricted areas of Crete (*Z. abelicea*) and Sicily (*Z. sicula*) (Di Pasquale et al., 1992). *Liquidambar orientalis* occurs in different areas (Fig. 1b). The vastest extension is located in the riparian forests of the southwesternmost Anatolia (area of Köyceğiz–Marmaris) but can also be found in northeastern Antalya (Akman et al., 1993). The third occurrence area is located along the Oronte River, close to Hatay. The two last localities significantly shortened since the Hellenic time during which ancient documents indicate that *Liquidambar* was abundant and intensely used for producing styrax (Amigues, 2007). *Pterocarya fraxinifolia* is still present in riparian forests along the Black and Marmara seas, being relatively abundant in the latter (Fig. 1b). It is also recorded in some localities near the Iskenderun Gulf (Fig. 1b). This tree also occurs in the above-mentioned Anatolian regions where *Zelkova* is living. *Cedrus libani* seems to be better distributed (Quézel and Médail, 2003): it abounds on the Taurus and Anti-Taurus massifs, although it is declining today (Fig. 1b). Few reduced populations persist on the back slope of the Pontic Ranges (region of Erbaa–Niksar; Fig. 1b).

To summarize, the present-day plant refuges in Anatolia are located on both latitudinal edges (Fig. 1b), between 42° and 40°N (*Pterocarya fraxinifolia*) and 38° and 36°N (*Liquidambar orientalis* and *Cedrus libani*), respectively. We must recall that *Pterocarya fraxinifolia* and *Zelkova carpinifolia* are also growing today in the nearby western Transcaucasia (Colchis plant refuge area; Denk et al., 2001).

3. Methods and materials

In this study, 786 pollen samples have been analysed from 13 sections (Fig. 1a): Ermenek, Burhanlı, Eceabat (D. Biltekin), İntepe (D. Biltekin and J.-P. Suc), Avadan and Karayayla (J.-P.

Suc), Site 380 (S.-M. Popescu, D. Biltekin, S. Boroi, J.-P. Suc), Seyitömer, Güven, Bayramhacılı, Akdağ, Güzelöz (N. Yavuz), Çatakbağyaka (G. Jiménez-Moreno) (Figs. 2, 3).

3.1. Pollen analysis

About 20-30 g of dry sediment was processed using acids (HCl35%, HF70%). Then, palynomorphs were concentrated using $ZnCl_2$ (density >2) and through sieved (10 μm). The final pollen-rich residue was mounted in glycerol. An almost similar technique but adding KOH to some samples was used for the localities Güvem, Akdağ, Seyitömer, Bayramhacılı, and Güzelöz (Yavuz-Işık, 2007, 2008; Yavuz-Işık and Toprak, 2010).

Pollen analyses result from counting a minimum of 150 pollen grains, excluding *Pinus*. A special effort was done in the botanical identification of pollen grains from late Cenozoic sediments since the 1970's under the initiative and training of one of us (J.-P.S.). For this purpose, a very accurate attention was done to pollen morphology with a continuous comparison between past and present pollen grains. The latter are examined from modern plant pollen grain collections. Their photographs were systematically indexed and a corresponding database has been developed, which benefits from continuous updating. Some regional photograph atlases (Europe, Southeastern Asia, Mediterranean) of modern pollen grains have also been regularly consulted. Scanning Electronic Microscope has been used for comparative examination of some past and modern pollen grains. This effort gave to the authors a very extensive experience in pollen morphology and knowledge of the past peri-Mediterranean pollen floras. In this study, we pay special attention to selected (often thermophilous/hygrophilous) taxa that have disappeared from Anatolia (*Avicennia*, Sapotaceae, Arecaceae, *Cathaya*, Taxodiaceae, *Nyssa*, *Engelhardia*, *Tsuga*, *Carya*, *Zelkova*, *Parrotia persica*) or are still present in the region (*Cedrus*, *Liquidambar*, *Pterocarya*) (Figs. 2, 3).

Fluorescence microscopy is commonly used as a reliable reworking index (Havinga, 1967; van Gijzel, 1967; Philips, 1972; Doláková and Burešová, 2007): "with increasing age and for a single type of palynomorph, the colours shift from blue-green, white or yellow and strong fluorescence to orange, red or brown and weak fluorescence". In order to test reliability of the Taxodiaceae pollen from the upper part of the series (2 m, 30.51 m, 49.47 m, 169.16 m), we performed a comparative examination using fluorescence microscopy also including samples from the middle and lower parts of the series (334.50 m: Middle Pleistocene; 976.99 m: late Miocene) where Taxodiaceae pollen is clearly not reworked. In the uppermost samples, comparison has been extended to *Artemisia* pollen which cannot be regarded as reworked. Examination was done using an AX10 Lab.A1 Zeiss microscope where fluorescence intensity has been adjusted between 56 and 72.

3.2. Pollen localities

The considered (twelve outcrops, one core) sections are dated by various methods (Figs. 2, 3). The Ermenek lacustrine sediments are ascribed to lower Miocene according to mammals and freshwater ostracods, being overlain by late Burdigalian marine deposits (Ilgar and Nemec, 2005). These sediments, deposited close to the sea level, have been uplifted (up to about 1000 m) since the middle Miocene. In the Güvem Basin, lacustrine diatomites and clays are exposed at *ca*. 1500 m in altitude and dated by Burdigalian mammals. They are inbedded within volcanic deposits comprised between about 20 Ma (base) and 18 Ma (top; Yavuz-Işık, 2008). The fluvio-lacustrine deposits of Çatakbağyaka (altitude: 500 m) are dated as Langhian after studying their mammal content (Sickenberg et al., 1975; Heissig, 1976). The Seyitömer series (*ca*. 1100 m in altitude) is also dated by mammals (Yavuz-Işık, 2007): its lower part (coal) is younger than 18 Ma (upper Burdigalian), its upper part is older than 11 Ma (Serravallian; Sen, 1997). The age of

the clayey pollen localities from the relatively high area of Nevşehir (Akdağ: 1100 m; Bayramhacılı: 1000 m; Güzelöz: 1500 m) is indicated by radiometry of associated ignimbrites: range of the Akdağ pollen flora is 9–8.3 Ma, that of Bayramhacılı 7.6–6.8 Ma, that of Güzelöz 4.5–3 Ma (Yavuz-Işık and Toprak, 2010). The low pollen floras of Burhanlı (12 m), Eceabat (60 m) and İntepe (180 m) come from marine clays dated by calcareous nannoplankton, from late Tortonian to earliest Zanclean (Melinte-Dobrinescu et al., 2009). The marine shale layers from Avadan (altitude: 110 m) and Karayayla (altitude: 150 m) are dated as early Zanclean according to planktonic foraminifers (Nazik, 2004). DSDP Site 380 (water depth: 2107 m) benefits from a robust calcareous nannoplankton biostratigraphy calibrating the high-resolution climatostratigraphy provided by the pollen record, which allows precise relationships with the reference oxygen isotope curve (Popescu et al., 2010). As a consequence, robust ages since 6 Ma are indicated in Figure 3.

4. Pollen floras

Pollen assemblages of the new localities are shortly reviewed to inform on their floristic content and vegetation significance. Variability is also indicated according to their geographic location and age.

4.1. Ermenek (early Miocene)

The Ermenek flora (Figs. 1a, 2) includes few pollen grains of very scarce megathermic elements (Sapotaceae, Euphorbiaceae, Rubiaceae) accompanied by some mega-mesothermic elements especially in the upper part of the section (Taxodiaceae, *Engelhardia*). Mesothermic elements (*Carya*, *Pterocarya*, *Liquidambar*, *Zelkova*[1]) are frequent to abundant in some samples. *Cathaya* is frequent in the lowermost part of the section, *Cedrus* is continuously abundant despite decreasing percentages at the top, both probably originating from the nearby Central Taurides. The Ermenek palaeolake was bordered by mesophilous forests replaced in altitude by coniferous woodlands dominated by *Cedrus* (with *Cathaya*, *Tsuga*, *Abies*, *Picea*). The continuous record of *Artemisia* suggests the early occurrence of steppe environments in this area.

4.2. Güvem (early Miocene)

This pollen flora (Figs. 1a, 2; Yavuz-Işık, 2008) is characterized by few megathermic taxa (Sapotaceae) and frequent mega-mesothermic plants (Cyrillaceae-Clethraceae, Taxodiaceae, especially *Engelhardia*). *Carya* is dominant among mesothermic trees with occurrences of *Pterocarya* and *Liquidambar*. Meso-microthermic (*Cathaya*) and microthermic (*Cedrus*) conifers are rarely represented, suggesting that no high relief existed at 18 Ma in this volcanic area. A mesophilous forest probably occurred around the Güvem palaeolake. Open environments were not important.

4.3. Seyitömer (early-middle Miocene)

This pollen flora (Figs. 1a, 2; Yavuz-Işık, 2007) includes very few megathermic (Sapotaceae) and mega-mesothermic (Taxodiaceae, *Engelhardia*) taxa. *Carya*, *Pterocarya*, *Zelkova*, *Liquidambar* and *Parrotia persica* are among the main mesothermic plants. *Cathaya* is present and *Cedrus* is very abundant, suggesting high-elevation conifer forest growing on nearby

[1] Note that *Zelkova* has only been considered as present when the when the pollen-analyst distinguished it from

mountain ranges. The local vegetation was a swamp forest during the Burdigalian (coal deposits) replaced by a mesophilous forest later on in the Langhian (clayey deposits). Conifer forest grew in altitude.

4.4. Çatakbağyaka (middle Miocene)

This pollen flora (Figs. 1a, 2; Jiménez-Moreno, 2005; Jiménez-Moreno et al., 2007) is highly diversified. This is shown by the occurrences of several megathermic (Euphorbiaceae, Rubiaceae, Sapotaceae, *Alchornea*, Passifloraceae, *Acacia*) and mega-mesothermic (Arecaceae, Celastraceae, *Distylium*, *Engelhardia*, Taxodiaceae) taxa and agrees with its assignment to the warmest phase of Miocene. Mesothermic plants include *Carya*, *Pterocarya*, *Liquidambar*, *Zelkova*, and *Parrotia persica*. *Cedrus* and *Cathaya* also occur, denoting some elevated relief in the region. Herbs constitute a significant part of the pollen assemblage indicating relatively open environments.

4.5. Nevsehir area: Akdağ, Bayramhacílı, Güzelöz sections (late Miocene–early Pliocene)

Three pollen floras document this time-interval in the central Anatolia Plateau: Akdağ, Bayramhacílı and Güzelöz (Figs. 1a, 2, 3; Yavuz-Işik and Toprak, 2010). The Akdağ pollen flora includes few mesothermic plants (with *Pterocarya*, *Parrotia persica*). *Cedrus* occurs in low percentages. A similar composition characterizes the Bayramhacílı pollen flora where only *Carya* and *Liquidambar* are present among the mesothermic plants. *Tsuga*, *Cathaya* and *Cedrus* occur in low percentages in this pollen record. *Pterocarya* is present at Güzelöz. *Artemisia* and other herbaceous pollen are abundant in these localities, documenting the ancient development of Anatolian steppes on the plateaus (Yavuz-Işik and Toprak, 2010).

4.6. The Dardanelles Strait area: Burhanlı, Eceabat, İntepe sections (late Miocene–earliest Pliocene)

Three pollen floras document this time-interval in the Dardanelles Strait area: Burhanlı, Eceabat and İntepe (Figs. 1a, 2, 3; Melinte-Dobrinescu *et al*., 2009). Mega-mesothermic plants are represented by low percentages of *Engelhardia* and Taxodiaceae. *Carya*, *Pterocarya*, *Liquidambar* and *Zelkova* are relatively frequent among the mesothermic plants. Altitudinal trees are represented by *Cathaya*, *Cedrus*, *Abies* and *Picea*. Their percentage increases significantly after the Messinian Salinity Crisis, well recorded in this area through fluvial erosion. This increase in altitudinal plants probably results from the uplift of the Ganos-Gelibolu Massif as a response to the blocking of the North Anatolian Fault before its propagation (Armijo et al., 1999; Melinte-Dobrinescu et al., 2009). The coastal area was characterized by open vegetation (Melinte-Dobrinescu et al., 2009).

4.7. Avadan and Karayayla (early Pliocene)

Plant diversity of the Avadan and Karayayla coastal pollen floras (Figs. 1a, 3; Jiménez-Moreno et al., 2007) is low, with Sapotaceae and Taxodiaceae as the only megathermic and mega-mesothermic representatives respectively. Mesothermic plants *Pterocarya*, *Liquidambar* and *Zelkova* also occur. *Cathaya* and *Cedrus* are present, coming from the Central Taurides mountain range. Local coastal vegetation was characterized by herbaceous plants.

4.8. Site 380 (late Miocene to Present)

DSDP Site 380 is a unique deep marine long pollen record covering the last 6 Ma (Figs. 1a, 3; Popescu, 2006; Popescu et al., 2010; Biltekin, 2010).

The simplified pollen diagram can be subdivided into three parts from the diversity viewpoint:

- *ca*. 6–3.37 Ma, 1020–703 m below the sea floor (bsf): forested vegetation dominated despite some forest retreats due to coolings marked by the initial expansion of *Artemisia* steppe (Popescu, 2006). Megathermic taxa were sporadic (*Avicennia*, Sapotaceae, *Amanoa*, *Fothergilla*, Sapindaceae, Acanthaceae). Mega-mesothermic plants were abundant (with mainly Taxodiaceae in large percentages, *Engelhardia*, Arecaceae, *Nyssa*, *Distylium*, *Microtropis fallax*). Mesothermic abounded (particularly deciduous *Quercus*, *Carya*, *Pterocarya*, *Liquidambar*, *Zelkova*, *Parrotia persica*). *Cathaya* and also *Tsuga* and *Cedrus* were almost continuously recorded, indicating the presence of high-elevation mountain ranges near the Black Sea shore.
- 3.37– *ca*. 1.22 Ma, 703–319 m bsf (Biltekin, 2010): most of the megathermic plants disappeared, except for *Avicennia* recorded at 412 m. This decrease in megathermic species is specifically well marked at 703 m, corresponding to the cooling at 3.37 Ma (Popescu et al., 2010). Another well-marked decrease in thermophilous species occurred at 2.62 Ma. This one was related to the earliest glacial cooling in the Northern Hemisphere (Popescu et al., 2010). This event was characterized by:
    - among the mega-mesothermic taxa: disappearance of Arecaceae, almost complete extinction of *Nyssa*, and strong decline in *Engelhardia* and Taxodiaceae;
    - among the mesothermic plants: disappearance of *Parrotia persica*, strong decline in *Liquidambar*, and weakening of *Carya*, *Pterocarya* and *Zelkova*;
    - scarcity of the meso-microthermic conifer *Cathaya* (despite a short interval of almost continuous record between 649 and 638 m);
    - relative strengthening of *Tsuga* and *Cedrus* (microthermic conifers).

  This interval was characterized by the alternation between mesophilous forest (warm phases) and steppes (cool phases) enriched in *Artemisia* at the onset of the 41 kyr North Hemisphere climatic cycles. Interglacials were characterized by peaks of deciduous *Quercus* and Taxodiaceae (*Glyptostrobus*) (Fig. 3). Taxodiaceae pollen grains were probably favoured in the water transport because these trees inhabited coastal areas where they extended during those warm periods (Popescu et al., 2010).
- 1.22 Ma–Present, 319 m bsf–hole top. There was a supremacy of *Artemisia* steppes over mesophilous forests whatever the climatic phase, glacial or interglacial. This vegetation characterized a period of progressive replacement (350–300 m) of the 41 kyr climatic cycles by 100 kyr cycles (Popescu et al., 2010). The survival of Taxodiaceae in this area is a crucial question to be discussed. Thermophilous taxa present a generally regressive trend:
    - *Engelhardia* progressively became rare and disappeared at 86 m. Taxodiaceae declined too during glacials but increased during interglacials up to practically disappear during the Last Glacial (30–17 m). Taxodiaceae reappeared at the Holocene but progressively declined up to Present;
    - *Carya*, *Pterocarya*, *Liquidambar* and *Zelkova* disappeared too;
    - *Cathaya* discontinuously reappeared (219–114 m depth) while *Cedrus* and mostly *Tsuga* became rarer.

5. Plant extinctions in the Northeastern Mediterranean region

Floral changes for the past 23 Ma are described in this study through a review of pollen records from the Northeastern Mediterranean area. This concerns thirty two more pollen records besides the ten ones described above. They are located within and nearby the North latitude intervals 36°–38° (SALI = South Anatolia latitudinal interval) and 40°–42° (NALI = North Anatolia latitudinal interval) (Fig. 4a, Table 1), where present-day plant relicts occur (Fig. 1b). We only used localities characterized by a reliable chronology and where pollen was classified using a botanical identification. We selectively used macrofloras to support the presence or absence of some taxa. The taxa selected for this review are those that are reliably identified in all the pollen floras: *Avicennia*, Sapotaceae, Arecaceae, *Nyssa*, *Engelhardia*, *Carya*, *Cathaya*, *Tsuga*, Taxodiaceae (non *Sciadopitys*), including those still living in Anatolia (*Pterocarya*, *Liquidambar*, *Cedrus*) or nearby (*Zelkova*, *Parrotia persica*). This comparison greatly benefited from the long Site 380 pollen record. We distinguished three classes of plants: those which do not grow today in the Northeastern Mediterranean region, those still occurring near Anatolia and those still growing in Anatolia. These plant's dynamics were examined and compared to the present-day geographic distribution of their living representatives.

5.1. Taxa today absent from the Northeastern Mediterranean region

The occurrence at Site 380 of occasional pollen grains of *Avicennia* at about 6 Ma, 4.8 Ma and 1.6 Ma is noteworthy (Figs. 3, 4b). Evidences of this mangrove tree on the northern Anatolian shoreline at 6 and 4.8 Ma are consistent with the presence of other megathermic taxa (*Amanoa*, *Fothergilla*, *Exbucklandia*, Sapindaceae, Loranthaceae, Acanthaceae; Popescu, 2006). The record of a single pollen grain at *ca*. 1.6 Ma is more questionable. Was *Avicennia* still growing in the area or is it an unusually very well-preserved reworked pollen? We must thus imagine a protected North Anatolian coastline with a propitious salinity context at least up to 3.37 Ma, or even later. In this region, occurrence of *Avicennia* is documented in the early Oligocene at Pullukcu, NW Turkey (İslamoğlu et al., 2010) and in the middle Miocene at Satovcha, SW Bulgaria, by one of us (J.-P.S.) in a floral context including Passifloraceae, Sapindaceae and Meliaceae (D. Ivanov, personal information). A Langhian occurrence of Avicennia has been recently reported by Kayseri-Özer (2014) on the Aegean Turkish shoreline near Kultak – Muğla – Milas area in the SALI (i.e., *ca*. 37°N latitude) without complete information on the data (Figs. 4a, 4c). Later, only the occasional records from Site 380 support the presence of *Avicennia* in the region. The presence of Sapotaceae is scarcely documented in Anatolia and at Site 380 up to the earliest Pliocene (Figs. 2, 3, 4b). Sapotaceae were found in the NALI at Ptolemais (Northern Greece; Figs. 4a-b, Table 1) up to *ca*. 4 Ma (Ioakim, 1984)[2]. Their extinction occurred at *ca*. 1.7 Ma in the SALI in the Citadel section (Zakynthos Island; Figs. 4a-c, Table 1; Suballyova et al., 1999; Subally et al., 1999).

Nyssa has not been recorded in the Anatolian Neogene (Fig. 2). It is scarcely documented between 6 and 5.6 Ma at Site 380 with other three limited occurrences at *ca*. 4.7 Ma, *ca*. 1.25 Ma and *ca*. 850 ka (Figs. 3, 4b). It is very rare in the NALI, with discontinuous occurrences up to about 4 Ma as documented at Ptolemais[2] (Fig. 4b; Ioakim, 1984). In the SALI, only the central Greece Mavradzei locality (12–11 Ma; Ioakim and Solounias, 1985) records *Nyssa* except for a brief occurrence at Zeli in the Samos Island (lower Pleistocene; Ioakim and Rondoyani, 1988) (Figs. 4a, 4c, Table 1).

Engelhardia is continuously recorded in Anatolia and abundant up to *ca*. 1.25 Ma at Site 380 (Figs. 2, 3). It decreased later on and its last occurrence is recorded at Site 380, within the Middle Pleistocene at *ca*. 200 ka (Figs. 3, 4b). Other NALI localities do not document its presence later than 4 Ma (last occurrence at Ptolemais[2]: Ioakim, 1984; Biltekin, 2010) (Fig. 4b),

[2] Chronology based on correlations with magnetostratigraphy of Van Vugt *et al*. (1998).

while those of the SALI show its presence up to 1.7 Ma at the Citadel of Zakynthos (Suballyova et al., 1999; Subally et al., 1999) (Fig. 4c).

Taxodiaceae display two pollen types (Erdtman, 1965): pollen of *Sciadopitys* has a unique morphology; pollen grains with an appendix (papilla) characterize the other genera (*Sequoia*, *Taxodium*, *Glyptostrobus*, *Metasequoia*, *Cryptomeria*, *Cunninghamia*, *Taiwania*, *Sequoiadendron*, *Athrotaxis*). The latter taxa are abundant in the sediments of Site 380 and usually found in the other studied localities (Figs. 2, 3). Identification of their pollen grain is possible at the genus level on the basis of (1) the size and shape of papilla and (2) the distribution and density of glomeruli constituting the sculpture observed at the scanning electronic microscope (Reyre, 1968; Jinxing and Yuxi, 2000). Pollen grains of Taxodiaceae from Site 380 show these morphological characters under the light microscope. This is confirmed at the scanning electronic microscope for many specimens from several samples (Plate I). The comparison at the scanning electronic microscope of the fossil pollen grains with pollen grains of the different Taxodiaceae genera shows that the Taxodiaceae pollen grains from Site 380 mostly belong to *Glyptostrobus* (Plate I, 1-4). This identification is in agreement with the many occurrences of *Glyptostrobus europaeus* in the Neogene macrofloras from the region (Kasaplıgil, 1977; Velitzelos and Gregor, 1990; Gemici et al., 1991; İnci, 2002). As discussed by Popescu et al. (2010), *Glyptostrobus* should have inhabited swamps along the southern Black Sea coastline during the last 6 Ma. *Glyptostrobus* went through two severe declines at about 1.2 and 0.5 Ma (Fig. 3), but might have survived in this area until recently. Within the NALI, only Site 380 documents persistence of Taxodiaceae later than 4 Ma (recorded at the top of the Ptolemais^2 series: Fig. 4b; Ioakim, 1984; Kloosterboer-van Hoeve, 2000; Biltekin, 2010). In the SALI, Taxodiaceae are recorded up to *ca*. 1 Ma at Tsampika (Figs. 4a, 4c, Table 1; Joannin et al., 2007). *A priori*, the record of Taxodiaceae pollen at Site 380 until the Holocene might be considered as resulting from reworking, as this family is absent today from the region. However, Taxodiaceae pollen grains are well-preserved throughout the section, particularly in the uppermost levels (Plate I, 11-12). In addition, Site 380 has been cored in a deep basin (2107 m of water depth) where input of terrigenous sediments by rivers is relatively weak. Sedimentation rate at Site 380 since 2.62 Ma (beginning of the glacial-interglacial cycles) is only 26 cm/kyr on average, which is very different from the 58 cm/kyr for the last 520 ka at hole PRGL1-4 in the Gulf of Lions (NW Mediterranean), mostly fed in terrigenous sediments by the Rhône River (Suc et al., in progress). Here, obviously reworked pollen grains represent at maximum 5% of the pollen content in present-day sediments (Beaudouin et al., 2007), less than 7% in sediments cored at hole PRGL1-4 for total pollen concentration generally lower than 2,000 grains/g of sediment. At Site 380, obviously reworked pollen grains are less than 3% for a total pollen concentration that comprised between 3,000 and 20,000 grains/g of sediment (Popescu, 2001). This comparison suggests that potentially reworked pollen grains at Site 380 are few.

Moreover, Taxodiaceae percentages at Site 380 covary with the mesothermic trees as illustrated by deciduous *Quercus* in Figure 3. Since 1 Ma (i.e. the uppermost 230 m of the series), glacial–interglacial alternations are more pronounced and Taxodiaceae percentages decreased significantly. Peaks in deciduous *Quercus* reflect warm phases (i.e., interglacials; Fig. 3) and it is almost continuously recorded and beyond suspicion of reworking. If resulting from reworking, Taxodiaceae pollen should have been expected to show an opposite pattern than that of deciduous *Quercus*, with maxima occurring during glacials when the Black Sea level dropped and land erosion and fluvial transport of reworked pollen grains were probably optimal according to the scenario developed by Lericolais et al. (2009, 2013) for the Last Climatic Cycle. Pollen data contradict such a model for transport and redeposition of Taxodiaceae pollen in the deep southwestern Black Sea during cold phases of the Late Pleistocene and Holocene. In addition, according to its location, Site 380 was not fed in terrigenous sediments by the powerful Danube River (Lericolais et al., 2013) but by short Thrace rivers and predominantly by the

Anatolian Sakarya River (Fig. 1a). Actually, Taxodiaceae appear to show a fluctuating pattern of progressive extinction within a frame of glacial–interglacial phases up to a very weak residual occurrence during the Holocene (Fig. 3).

At 2 m and 30.51 m depth, well-preserved Taxodiaceae pollen grains (Pl. II, Figs. 1, 7) respectively ascribed to Holocene and Late Pleistocene (Fig. 3) show a yellow to orange relatively strong fluorescence (Pl. II, Figs. 2, 8). They cannot be absolutely considered as non-reworked but almost probably autochthonous *Artemisia* pollen grains (Pl. II, Figs. 3, 9) show a similar response to excitement (Pl. II, Figs. 4, 10). No conclusive interpretation can be expressed from these specimens. Two other similarly preserved Taxodiaceae pollen grains (Pl. II, Figs. 13, 17) have been observed at 169.16 m depth (Middle Pleistocene). They show a yellow strong fluorescence (Pl. II, Figs. 14, 18) such as pollen of *Artemisia* (Pl. II, Figs. 15, 16) and must be regarded as autochthonous. At 334.50 m depth (lower Pleistocene), Taxodiaceae pollen displays a yellow and moderate fluorescence (Pl. II, Figs. 19, 20). At last, Taxodiaceae pollen from Messinian (976.99 m depth) shows a yellowish–orangy relatively weak fluorescence (Pl. II, Figs. 21, 22). The observed fluorescence gradient from 976.99 to 169.16 m depth is in agreement with the age range from Messinian to Middle Pleistocene (*ca*. 0.5 Ma). Equivalence of both Taxodiaceae and *Artemisia* with respect to fluorescence unquestionably supports that Taxodiaceae pollen grains are not resedimented. Only authenticity of the uppermost Taxodiaceae specimens could be debated. However, their almost similar even stronger fluorescence compared to that of the *Artemisia* specimens incline us to consider that they can reflect some residual coastal Late Pleistocene to Holocene communities. We feel that their very good preservation (Pl. I, Figs. 11, 12; Pl. II, Figs. 1, 7) may be regarded as a non-decisive argument. However, the occurrence in Holocene and Late Pleistocene layers of some less preserved Taxodiaceae (Pl. II, Figs. 5, 11) pollen with an orangy weak fluorescence (Pl. II, Figs. 6, 12) indicates that actually reworked distinguishable specimens are mixed with low quantity well-preserved pollen grains that we have counted as probably non reworked ones.

Therefore, we must objectively consider that occurrence of non-reworked Taxodiaceae pollen grains cannot be neglected in the uppermost layers of Site 380. The probability is conceivable that relictuous communities of *Glyptostrobus* have inhabited coastal swamps of the south Black Sea coastline up to until sometime during the Holocene (Fig. 4b). Some cores from the Marmara Sea (MAR98-9: Fig. 4a; Table 1; Mudie et al. 2002; MD01-2430: Valsecchi et al., 2012) and from the southern Black Sea (B7: Fig. 4a; Table 1; Mudie et al. 2002; 22-GC3: Shumilovskikh et al., 2012) provided a pollen flora documenting the Holocene vegetation in the region. These records do not mention Taxodiaceae pollen and, according to the available information, we can propose three possible alternate explanations as follows:

- the analysed cores were too far to the West (Marmara cores) and to the East (Black Sea cores) from the relictual *Glyptostrobus* localities which could have been confined around the mouth of the Sakarya River (Fig. 1a);
- pollen-analysts may have found Taxodiaceae pollen grains in these records and a priori put them in the stock of reworked pollen, an understandable behaviour for lack of Pleistocene step back that is filled in by our study at Site 380;
- at last, pollen-analysts may have been unsure in identifying Taxodiaceae pollen.

At Site 380, *Cathaya* pollen is relatively abundant during two time-intervals: 6–3 Ma and 950–380 ka (Figs. 3, 4b). Considering the other localities within the NALI, its presence is confirmed at *ca*. 4 Ma (Fig. 4b) at Ptolemais[2] (Ioakim, 1984; Kloosterboer-van Hoeve, 2000; Biltekin, 2010). In several other localities, it has not been identified yet as such but it could be present at Tenaghi Philippon[3] (Northern Greece; Fig. 4a, Table 1) under the names *Podocarpus* at *ca*. 1.1 Ma and/or *Pinus* haploxylon type, almost continuously present up to 850 ka and

[3] The chronology relative to Tenaghi Philippon is from Tzedakis et al. (2006).

sporadically indicated at 325 ka, 50 ka, 30–40 ka (Fig. 4b; Wijmstra, 1969; Wijmstra and Smit, 1976; Van der Wiel and Wijmstra, 1987a). The SALI displays the presence of *Cathaya* up to at least 1 Ma, as documented at Tsampika (Fig. 4c; Joannin et al., 2007).

Carya is almost continuously recorded up to 380 ka and sporadically until *ca*. 2 ka at Site 380 (Figs. 3, 4b). Within the NALI, the last evidences of *Carya* at Tenaghi Philippon[3] are recorded at about 900 ka (Van der Wiel and Wijmstra, 1987b). This contrasts with its occurrence in the core MAR98-9 (eastern Marmara Sea; Fig. 4a, Table 1) during the last 4 ka (Mudie et al., 2002) (Fig. 4b). *Carya* is rarely documented in the SALI from 4.5 Ma to 1 Ma (last occurrence at Tsampika; Joannin *et al*., 2007) (Fig. 4c).

Tsuga is continuously recorded at Site 380 up to 1.27 Ma and sporadically found until 230 ka (Figs. 3, 4b). Within the NALI, *Tsuga* is continuously recorded at Tenaghi Philippon[3] up to 1.1 Ma and sporadically until 700 ka (Fig. 4b; Van der Wiel and Wijmstra, 1987a, 1987b).

5.2. Taxa absent today from Anatolia but still living in a nearby region

Zelkova pollen is not always distinguished from that of *Ulmus*. We identified *Zelkova* specimens from Site 380, where it is continuously recorded up to 1.22 Ma and sporadically up to 150 ka, using its morphological criterions concerning ectexine: thicknening around the pores and proeminent sculpture (Kuprianova, 1965; Figs. 3, 4b). At Tenaghi Philippon[3], *Zelkova* is clearly documented until 450 ka (Van der Wiel and Wijmstra, 1987a), but only mentioned up to 340 ka (Wijmstra and Smit, 1976; Wijmstra, 1969). Tzedakis et al. (2003) show sporadic occurrences of *Zelkova* during the Last Interglacial between 133 and 115 ka at Ioanina (western Greece; Fig. 4a, Table 1), which would constitute the youngest records in the NALI (Fig. 4b). The presence of *Zelkova* is undoubtedly documented in the SALI until 0.98 Ma, with additional potential occurrences between 650 and 300 ka at Megalopolis (west Peloponnesous; Figs. 4a, 4c, Table 1; Okuda *et al*., 2002) and last localized robust occurrences between 4 and 3 ka at holes OEN 1 and 2 from the Acheloos Delta (outlet of the Corinth Gulf; Figs. 4a, 4c, Table 1; Fouache et al., 2005). The recent last occurrences of *Zelkova* pollen in both latitudinal intervals are in agreement with its survival in Crete (Quézel and Médail, 2003), close to Van Lake in southeastern Turkey (see above) and western Transcaucasia (Denk et al., 2001).

Parrotia persica's pollen grain is not frequently identified because its thin membrane (exine) is often poorly preserved (see photographs of modern and fossil pollen grains of *P*. *persica* in: Naud and Suc, 1975; Bińka et al., 2003; Leroy, 2007). However, it has been reliably recorded up to 3.85 Ma at Site 380 (Figs. 3, 4b). Also it has been reported at Tenaghi Philippon[3] until 830 ka (Fig. 4b; Van der Wiel and Wijmstra, 1987a, 1987b). *P*. *persica* has been found up to 980 ka in the SALI, at Tsampika (Figs. 4c; Joannin et al., 2007). Its retreat to its present populations in few more or less isolated small areas in Iran (Wendelbo, 1968; Sefidi et al., 2011) thus appears to be relatively ancient. Pollen records show the occurrence of *Parrotia persica* in the southern Caspian region during the entire Holocene (Leroy et al., 2011, 2013).

5.3. Taxa still living in the Northeastern Mediterranean region

Arecaceae have been continuously recorded up to 3.37 Ma at Site 380 (Figs. 3, 4b). The youngest occurrence of Arecaceae in the other localities of the NALI is at about 4.2 Ma in the Nestos 2 hole (Figs. 4a-b, Table 1; Drivaliari, 1993; Jiménez-Moreno et al., 2007). In the SALI, Arecaceae (cf. *Chamaerops*) have been recorded between 4 and 3 ka at holes OEN 1 and 2 from the Acheloos Delta (Figs. 4c; Fouache *et al*., 2005). Arecaceae survived until today in this latitudinal area. *Phoenix* is still present in Crete and southern Anatolia (*P*. *theophrasti*) and the

Mediterranean palm *Chamaerops humilis* occurred in Crete until recently (Quézel and Médail, 2003).

Pterocarya is continuously recorded in Anatolia during the Miocene and Pliocene (Figs. 2, 3). At Site 380, it becomes rare by 1.26 Ma and disappeared at 400 ka (Figs. 3, 4b). At Tenaghi Philippon[3], it becomes rare at 730 ka and disappeared at 510 ka (Wijmstra and Smit, 1976; Van der Wiel and Wijmstra, 1987a, 1987b). Very interesting is the pollen record from the Black Sea core BS7 (Fig. 4a, Table 1) where *Pterocarya* is rare until 7 ka and then relatively frequent up to Present (Mudie et al., 2002). Therefore, its occurrence in the NALI is documented until today (Fig. 4b), as also shown by Leroy et al. (2009, 2010) in northwestern Turkey. In the SALI, it became rare at 980 ka and disappeared at about 400 ka (Fig. 4c). This is indicated by the Megalopolis pollen record (Okuda et al., 2002) and is consistent with the present residual occurrence area of *Pterocarya*, larger in northern than in southern Anatolia (Fig. 1b).

Liquidambar pollen records indicate a similar Miocene and Pliocene history than *Pterocarya*, but it is relatively less abundant (Figs. 2, 3). At Site 380, its almost continuous presence ends at 1.28 Ma and it disappeared at 270 ka (Figs. 3, 4b). It is less abundant in the other localities from the NALI where it disappeared at 480 ka as recorded at Tenaghi Philippon[3] (Fig. 4b; Wijmstra and Smit, 1976; Van der Wiel and Wijmstra, 1987a, 1987b). In the SALI, *Liquidambar* pollen is more abundant up to 1 Ma (Tsampika; Joannin et al., 2007) and is not recorded after 300 ka (Megalopolis; Okuda et al., 2002) (Fig. 4C). *Liquidambar* is not continuously and abundantly documented. This is not surprising, as *Liquidambar* pollen is underrepresented in the pollen spectra (Brush and DeFries, 1981). Therefore, its absence from both NALI and SALI during the late Quaternary is not in contradiction with its present-day occurrence in southwestern Anatolia and in the island of Rhodes (Fig. 1b).

Cedrus pollen is abundant during the Miocene in Anatolia, particularly at Ermenek (Fig. 2). It is also relatively abundant at İ ntepe (Fig. 3) and Site 380 where it is almost continuously recorded up to 1.27 Ma and more discontinuously occurs until Present (Figs. 3, 4b). *Cedrus* pollen has been discontinuously to continuously recorded during the Last Glacial in southern Europe where such occurrences have been considered as resulting from long wind transport (Magri and Parra, 2002). Such pollen contaminations may have also affected the uppermost 60 m of Site 380. However, present-day *Cedrus* survivals in northern Turkey (Erbaa–Niksar; Fig. 1b) lead to moderate this probability in the region. *Cedrus* is frequent up to about 4 Ma at Ptolemais[2] (Ioakim, 1984; Kloosterboer-van Hoeve, 2000; Biltekin, 2010). It is almost continuously recorded up to 1.02 Ma at Tenaghi Philippon[3] and some occurrences are observed at 700 ka and 570 ka (Wijmstra and Smit, 1976; Van der Wiel and Wijmstra, 1987a, 1987b). *Cedrus* is present at 8.5 ka at Lake Maliq (Albania; Fig. 4a, Table 1; Denèfle et al., 2000). It discontinuously occurs during the last 10 ka in cores MAR98-9 and BS7 (Mudie *et al*., 2002). As a consequence, one may consider that *Cedrus* became rare in the NALI since 1 Ma but may have survived here until very recently (Fig. 4b) as shown by Leroy et al. (2009, 2010) in northwestern Turkey. In the SALI, *Cedrus* pollen is continuously recorded with significant percentages until 1 Ma (Tsampika; Joannin *et al*., 2007). Percentages decreased later, but it was almost continuously found during the last 48 ka in core C69, with some increases during the 43–36 ka and 25–6 ka intervals (SW Aegean Sea; Fig. 4a, 4c, Table 1; Geraga et al., 2005). The occurrence observed in the Acheloos Delta (core OEN1) at *ca*. 9 ka (Fouache et al., 2005) is to be considered in this context. Today, *Cedrus* includes four species: *C. deodara*, *C. atlantica*, *C. libani* and *C. brevifolia*. Their pollen grains show a homogenous morphology, however some distinctive characters have been indicated by Aytuğ (1961): they concern the cappa which is a little thicker in *C. deodara*, thinner in *C. atlantica*, with lateral crests in *C. libani* and *C. brevifolia* (Plate III, 1-4). Well-preserved *Cedrus* pollen grains from Anatolia display some homogeneity, with a relatively thick cappa and commonly lateral crests (Plate III, 5-12). A reconstructed *Cedrus* phylogeny (molecular clock) places the divergence between *C. atlantica* and the couple *C. libani*

– *C. brevifolia* at about 19 Ma, significantly after that with *C. deodara* (*ca*. 55 Ma) and prior to that within the couple *C. libani – C. brevifolia* (*ca*. 7 Ma) (Qiao et al., 2007). Accordingly, we may consider that the Neogene pollen grains of *Cedrus* recorded in Anatolia refer to the couple *C. libani – C. brevifolia* for the oldest floras (Ermenek, Catakbağyaka, Seyitömer) and to *C. libani* for the younger ones (İntepe, Site 380). Therefore, *Cedrus* has continuously been documented in the area for a very long time and validates its long-time continuous abundance on the mountain areas bordering the Anatolian Plateau and its elimination from the northern and western margins by human disturbance. The isolated and scattered populations of *Cedrus* near Niksar and Erbaa (Fig. 1b), whose origin was questioned by several authors (Pons, 1998; Quézel and Médail, 2003; Boydak and Çalikoğlu, 2008), are probably the remnants of a past larger distribution of *Cedrus* in northern Anatolia. Therefore, we believe that now there is enough data to support that present-day *Cedrus* forests were more widespread in the past (Anşin and Küçük, 1990).

6. Discussion

6.1. Compared extinctions in Anatolia, Europe Mediterranean region, and western Transcaucasia

The past 23 Ma floral history of northern Anatolia is accurately documented by pollen data from this area (Figs. 2, 3), completed by many other localities in the more extended NALI (northern Greece and Bulgaria) (Fig. 4b). Some taxa became extinct from northern Anatolia during the Pleistocene (*Engelhardia*, *Cathaya*, *Tsuga*, *Zelkova*, *Liquidambar*) or later on, during the Holocene (*Glyptostrobus*, *Carya*) probably related with human disturbance (Fig. 4b). Two taxa, *Pterocarya* and *Cedrus*, persisted in this area until today. NALI (Fig. 4a) can be considered as a refuge area at least since the upper Pliocene (occurrences of *Avicennia*? *Nyssa*? *Engelhardia*, *Glyptostrobus*, *Cathaya*, *Tsuga*). Today, climate in coastal northern Anatolia (Şensoy and Ulupınar, 2008) is temperate and humid almost continuously through the year: mean annual temperature comprised between 9 and 15°C, annual precipitations between 600 and 1200 mm with a maximum of 2200 mm to the East. Spring is the season with minimum rainfall. Such conditions are caused by conjugated humid air masses coming from the West and Northwest (Atlantic Ocean) and cold and dry air masses originating from Siberia, which get moisture over the Black Sea. Quantified climatic conditions at 5 Ma according to pollen data from Site 380 indicate a mean annual temperature at 17.3°C (range: 15.6–19.8°C) and annual precipitations at 1100 mm (range: 680–1550 mm) (Fauquette et al., 2006). Persistence of the last thermophilous taxa here (including those still present today) such as *Engelhardia*, *Carya*, *Zelkova* and *Pterocarya*, suggests that temperature and precipitations did not decrease too much in the region (or at least in certain refuge areas) during the Pleistocene glacial stages. Here, we used the present climatic distribution of plant species that occurred in this area during the Neogene in an attempt to delimit the range of climatic parameters during the Quaternary. For example, *Engelhardia*, the first of the four mentioned plants to disappear (200 ka at Site 380), lives today mainly in China where it requires a mean annual temperature that is comprised between 5.4°C and 24.8°C, a minimum temperature of the coldest month of -2.1°C and mean annual precipitations between 741 and 3495 mm (Fang et al., 2011). *Carya,* which was the last to disappear, includes some modern species in North America that tolerate low mean annual temperatures between 2 and 5°C (Thompson *et al*., 2000). Among the four Chinese species, *C. cathayensis* tolerates up to -0.4°C as mean temperature of the coldest month (Fang et al., 2011). The record of Taxodiaceae pollen grains at Site 380 until the Holocene is not problematic either as *Glyptostrobus pensilis* inhabits today lake shores or marine coastlines in regions of China and

Vietnam under warm and humid climatic conditions: mean annual temperature around 18.8°C (range: 10.6–23°C), mean temperature of the coldest month of 9°C (range: -0.2–15.2°C), mean temperature of the warmest month of 27.6°C and an annual precipitation of 1526 mm (range: 950–2148 mm) (Fang et al., 2011).

The history of the flora in southern Anatolia is discontinuously documented by pollen data from about 23 Ma to 5 Ma (Figs. 2, 3) and is fortunately completed by data from some Quaternary localities in the SALI (southern Greece) (Fig. 4b). Available data are not continuous enough to reconstruct a very complete story of the flora in southern Anatolia as in northern Anatolia. However, pollen data seem to be very reliable and relatively recent pollen records from SALI support the persistence until today of Arecaceae, *Liquidambar*, *Pterocarya* and *Cedrus*. This also applies to *Zelkova*, which also grows today in Crete and southeastern Turkey (Van Lake) (Fig. 4c). Today, climate of coastal region in southern Anatolia (Şensoy and Ulupınar, 2008) is greatly seasonal with mild and humid winters opposed to warm and dry summers: mean annual temperature comprised between 16 and 20°C and annual precipitations between 600 and 1400 mm, with some areas between 400 and 600 mm or even less. Such conditions are controlled by warm and dry air masses coming from North Africa, which can get some moisture over the Mediterranean Sea. The plant relics living at low altitude in southern Anatolia such as *Phoenix theophrasti* (Arecaceae), *Pterocarya fraxinifolia* and *Liquidambar orientalis* find the necessary humidity in riparian forest environments (Quézel and Médail, 2003). On the contrary, *Cedrus libani*, less demanding of high temperatures, generally grows today between 800 and 2100 m, with mean annual temperature ranging from 6 to 12°C, where it finds the necessary humidity (annual precipitation: 600–1200 mm with rainless summers) (Boydak and Çalikoğlu, 2008). The higher temperature range requirements of the relictuous populations of *Cathaya argyrophylla* in southern China (mean annual temperature: 13.4–18°C; Fang et al., 2011) could contribute to explain its extinction in the region. Nevertheless, *Tsuga* might have persisted here for longer time but could have disappeared because of competition with other conifers such as *Cedrus*, more tolerant to dryness.

Accordingly, it appears that two plant refuge areas were sketched out during the Quaternary at the far North and South of Anatolia, respectively. The coastal Black Sea region today seems to be very impoverished (Quézel and Médail, 2003), maybe because of anthropogenic disturbance (Kaya and Raynal, 2001). Southern Anatolia can be considered as a more propitious refuge area thanks to the occurrence of South-facing mountains that provided elevated humidity in warm valleys.

A review of the extinction history of four very significant taxa representing different bioclimatic plant communities (*Avicennia*: megathermic taxon; *Engelhardia*: mega-mesothermic taxon; Taxodiaceae: mega-mesothermic taxa inhabiting swamps; *Carya*: mesothermic taxon) in Western Europe, North Africa and Near East is given below. The age of their extinctions from these regions during the late Cenozoic is relatively well constrained (Fig. 5).

Avicennia (Verbenaceae) is a mangrove tree that grows today in coastal areas of the intertropical zone. It can be the only representative of mangrove ecosystem in some extra tropical areas (Fig. 5a; Tomlinson, 1986). Because of its relatively big size and entomophilous pollination, this pollen is generally rare in marine coastal sediments and indicates, when it is recorded, proximity to mangrove ecosystem (Thanikaimoni, 1987). According to its last occurrences in pollen records (Fig. 5b), *Avicennia* disappeared first from the northern Mediterranean coastlines (Jiménez-Moreno, 2005), probably as a result of the middle Miocene marine regression and global climate cooling (Zachos et al., 2001). Then, *Avicennia* persisted in the south Mediterranean shorelines with an extinction gradient from the West to East. The residual *Avicennia* mangrove on the North Anatolia coastline (until 4.8 Ma, even 1.6 Ma?) must be considered as an actual refuge if compared to its absence at the same time on the southeastern Mediterranean shoreline despite a floristic assemblage rich in megathermic elements (boreholes

Naf 1 and 2 offshore the Nile Delta and Gan Yavne 5 in Palestine: Drivaliari, 1993; Fauquette et al., 2006) close to its present-day presence along the Red Sea. Some other megathermic plants have been recorded in western Transcaucasia up to the end of the early Pliocene (Shatilova et al., 2011).

Engelhardia (Juglandaceae) is a subtropical tree, common in Southeast Asia (Fig. 5c; An-Ming, 1982). Its pollen is frequent to abundant in the European Miocene (Bessedik, 1985; Jiménez-Moreno and Suc, 2007; Jiménez-Moreno et al., 2008). The genus shows an extinction pattern during the Pliocene and early Pleistocene with decreasing ages from Northern to Southern Europe (Fig. 5d), in relation with the Northern Hemisphere temperature evolution (Tiedemann et al., 1994; Popescu et al., 2010). However, *Engelhardia* survived later in the southern Mediterranean (Fig. 5d) probably because of persisting high temperature but disappeared probably because of increasing dryness (Suc et al., 1995b). *Engelhardia* persisted up to Middle–Late Pleistocene in two areas, the West Adriatic and North Anatolia coastlines (Fig. 5d), probably milder and more humid areas. The last pollen evidence of *Engelhardia* in western Transcaucasia is reported in the early Middle Pleistocene (0.6–0.5 Ma; Fig. 5d) by Shatilova et al. (2011).

Two genera of the Taxodiaceae family inhabit subtropical to warm-temperate marine coastal or lacustrine swamps: *Taxodium distichum* (Northeast America) and *Glyptostrobus pensilis* (Southeast China) (Fig. 5e; Sternitzke, 1972; Fang et al., 2011). Their pollen is not always distinguished from each other and are usually classified as Taxodiaceae with papilla, leading to some imprecision in reconstructing the history of Taxodiaceae swamps in Europe, mainly constituted by *Glyptostrobus* if we refer to plant macroremains (Kovar-Eder et al., 2006). In Figure 5f we show the last record of all the Taxodiaceae pollen grains with papilla. On the whole, the pattern of extinction of these Taxodiaceae from Europe is almost similar to that of *Engelhardia* but at a younger time, during the earliest Pleistocene climatic cycles (Figs. 5d, 5f). A similar interaction is revealed between decrease in temperature and increase in dryness, opposing the North and South Mediterranean shorelines. Another opposition in humidity is particularly expressed on both edges of the Eastern Pyrenees with about 2 Myrs of delay on the more humid southern slope (Fig. 5f). As previously, two refuge areas of Taxodiaceae swamps are identified for the Middle Pleistocene, the Apeninnes-Adriatic area and the southwestern Black Sea area. Coastal Colchis is a part of the latter refuge area, where Shatilova et al. (2011) place the last record of lowland Taxodiaceae in the older part of the Last Glacial (ca. 50 ka; Fig. 5f), according to both pollen and macroremain evidences.

Carya is a warm-temperate genus requiring high humidity, distributed today in two disconnected areas, Northeastern America and Eastern China (Fig. 5g; An-Ming, 1982; Thompson et al., 2000). Its extinction from Europe occurred a little later than that of Taxodiaceae, in relation with the repeated coolings of the Middle Pleistocene, earlier in Northern Europe, forced by decrease in temperature, and Northern Africa, forced by increase in dryness (Fauquette et al., 1998; Klotz et al., 2006; Feddi et al., 2011; Fig. 5h). A refuge area has been identified in southern France up to the Last Glacial (Suc et al., in progress) and it persisted in northern Anatolia until the Holocene (Fig. 5h). Similarly, the last record of *Carya* pollen in western Transcaucasia is in the early Last Glacial (*ca*. 50 ka; Shatilova et al., 2011; Fig. 5h), that illustrates the decline of the northern Anatolia refuge area to which it belongs.

6.2. Evolution of Northern – Southern Anatolia and nearby western Transcaucasia plant refuge areas

Fossil records suggest that the Colchis (western Transcaucasia) plant refuge area experienced almost the same timing in thermophilous/hygrophilous plant extinctions than the nearby northern Anatolia. They will be grouped in the following synthesis.

6.2.1. Changes in the location of thermophilous and hygrophilous plant refuges through time

Location of plant refuges in Europe and surrounding regions is taking shape as the knowledge progresses on clarifying processes of restriction *vs*. enlargement of their distribution areas and the causes of their extinction (Milne and Abbott, 2002; Svenning, 2003; Leroy, 2007; Leroy and Arpe, 2007).

An inventory of present-day plant refuges within the Mediterranean region has been drawn up by Quézel and Médail (2003). Some relativity of the notion of plant refuge area follows from this study, according to the climatic conditions that the relict taxa withstand. However, our investigation at the scale of the whole Mediterranean region focuses on some emblematic thermophilous and/or hygrophilous trees. Meso-microthermic (*Cathaya*) and microthermic (*Cedrus*, *Tsuga*) trees will be dealt in forthcoming syntheses.

Lower-middle Miocene pollen records from Anatolia (Fig. 2) do not show significant differences with coeval pollen floras from Western Europe. Accordingly, Anatolia cannot be considered as a plant refuge area before the early Pliocene. The onset of the status of Anatolia as a thermophilous and/or hygrophilous plant refuge area may result from increasing monsoon influence (and associated summer rainfall) over the northeastern Mediterranean region (Popescu et al., 2006). At the early Pliocene, Anatolia was already split into two plant refuge areas, on its North and South coastlines, respectively. This disjunction is signalled by the oldest evidence of development of *Artemisia* steppe in the Tortonian deposits from Akdağ and Bayramhacılı (Yavuz-Işik and Toprak, 2010), probably resulting from the uplift of the Central Anatolian Plateau which started at *ca*. 8 Ma in its southern margin (Cosentino et al., 2012). The northward development of the Anatolian *Artemisia* steppe is then recorded at *ca*. 5.7 Ma at Site 380 (Popescu, 2006). Based on a vegetation numerical models with some control by palaeofloras, the presence of humid areas, which may have protected thermophilous and/or hygrophilous trees both on the northern and southern coastlines of Anatolia is indicated by François et al. (2011) for the late Miocene and Arpe et al. (2011) for the Last Glacial Maximum.

A comparative reconstruction of plant refuge areas at a Eurasian scale is attempted in Figure 6 for some selected taxa or groups of taxa at different time slices until Present. During the early Pliocene, northern Anatolia and western Transcaucasia appear to have been refuge areas for megathermic plants as well as Sicily, northern Africa and southern Iberia (Fig. 6a). The nearest present refuge areas are located in the Canary Islands and along the Red Sea shoreline, which is the nearest area to be inhabited by *Avicennia* (Fig. 6a).

The Central Mediterranean (from Tunisia to cental Adriatic Sea) and northern Anatolia must be regarded as early Pleistocene refuge areas for Taxodiaceae (mostly inhabiting coastal swamps), which persisted up to the Holocene in the latter (Fig. 6b). Many researchers have questioned the long-time survival of Taxodiaceae in this region as its pollen has often been considered as "mostly, if not entirely, reworked" in Caspian Holocene and Pleistocene sediments (Richards et al., 2011), although this opinion has been recently moderated in admitting possible relict populations (Richards et al., 2014). The age of disappearance of Taxodiaceae in this region was indeed considered as unknown, until the record of their decline and extinction in Site 380 (Fig. 3). And yet occurrence of Taxodiaceae in the residual Paratethys (southern Black Sea) until the early Last Glacial is supported by pollen and macrofloral records from western Transcaucasia (Shatilova et al., 2011; Fig. 6b). A highly fragmented Taxodiaceae distribution from the Near East to China is hence suggested for the late Quaternary.

During the Holsteinian (Late Pleistocene: *ca*. 0.4 Ma), several of the emblematic mesothermic and/or hygrophilous trees *Carya*, *Pterocarya*, *Zelkova*, *Liquidambar* and *Parrotia persica* invaded a very large territory in Europe (Bińka et al., 2003; Kondratienė and Šeirienė, 2003; Gerasimenko, 2008; Koutsodendris et al., 2010), greatly beyond their present-day residual biotopes scattered in the Central Mediterranean and Middle East (Fig. 6c).

These significant examples suggest that the evolution of refuge areas of thermophilous and/or hygrophilous plants must be understood as successive restrictions and fragmentations of former populations. The status of a geographic region as plant refuge area must only be considered as a shot at a given time, being highly evolutive with respect to fragility of ecosystems submitted to climatic changes, possibly diseases in fragmented areas and more recently by human disturbance (Willis and Niklas, 2004; Leroy, 2007; Leroy and Arpe, 2007).

6.2.2. Causes of evolution of thermophilous-hygrophilous plant refuges

There are several more or less connected causes of the retreat and disjunction of geographic areas occupied by thermophilous and/or hygrophilous plants:

- the long-term physiographic evolution of the Mediterranean and surrounding regions characterized by the onset of West-East barriers restraining even preventing the North-South migrations of plants in relation with temperature and humidity fluctuations (mountains: Pyrenees, Alps, Apennines, Hellenids, Carpathians, Taurids, Caucasus; Mediterranean Sea and reducing-scattering Paratethys; semi-deserts and deserts: Central Iberia, Anatolian Plateau, Sahara, Arabia) (Suc et al., 1995a). This is very different than in North America, where similar natural barriers are rather North-South oriented;
- the climatic changes, characterized by repeated more and more severe coolings and arid periods and less intense warmings that developed since 5.08 Ma (Combourieu-Nebout, 1990; Suc et al., 1995a; Suc and Popescu, 2005; Leroy, 2007; Joannin et al., 2008, 2011; Bertini et al., 2010; Popescu et al., 2010; Suc et al., 2010) causing also the growth of dry plant ecosystems;
- the onset of a Mediterranean seasonality, producing the extinction of hygrophilous species not adapted to a dry season (Suc, 1984);
- probably the increased frailty of plants suffering unfavourable conditions in the refuge places;
- at last, human activities, leading to extinction of greatly weakened residual communities of thermophilous and/or hygrophilous trees.

With 17.3°C as mean annual temperature, 7°C as mean temperature of the coldest month, 25.5°C as mean temperature of the warmest month, 1100 mm as annual precipitation (Fauquette et al., 2006), the reconstructed climatic conditions for Site 380 at the earliest Pliocene were less convenient than the present-day climatic conditions in which *Glyptostrobus pensilis* occurs (Fang et al., 2011). In addition to uncertainty on palaeoclimate reconstructions, it is possible that the *Glyptostrobus* fossil species (*G. europaeus* according to palaeobotanists; Kasaplıgil, 1977; Velitzelos and Gregor, 1990; Gemici et al., 1991; İnci, 2002), which probably lived in the Mediterranean region, was less demanding in terms of temperature and precipitation than the modern *G. pensilis* if comparing its life conditions (Fang et al., 2011) and Zanclean reconstructions by Fauquette et al. (1998) in the Northwestern Mediterranean. Global coupled simulations indicate a decrease of the mean annual temperature of 3–4°C in Anatolia during the Last Glacial Maximum (Kim et al., 2008; Schmittner et al., 2011) with a low increase in meridional heat flux and a slight lowering in summer rainfall, both with respect to Present (Kim et al., 2008). Arpe et al. (2011) obtained mean temperatures that are comprised between -0.1 and -5°C for winter and 10 and 20°C for summer for the same period (T106EH5 simulations). Such optimal glacial conditions could have allowed persistence of small and isolated populations of *Glyptostrobus* along the south Black Sea shoreline. Now, protected swampy Taxodiaceae individuals are usually cultivated in European private and botanical gardens up to high latitudes. A significant example of acclimatization is observed around the Nantua Lake in the Jura Massif (46°9’19”N, 5°35’59”E, altitude 475 m) where they have been introduced in the late eighties. The trees flourish and reproduced into several distant colonies under relatively low temperature

but humid conditions: 10.3°C as mean annual temperature, 1°C as mean temperature of the coldest month, 20°C as mean temperature of the warmest month, 1700 mm as annual precipitation (Auffray et al., 2011). Adaptation of specimens of swampy Taxodiaceae to such hard climatic conditions suggests that *Glyptostrobus* could have survived on the south Black Sea shore during past glacials. In addition, the Anatolian *Glyptostrobus* survival might have benefited from some reinforcement of the monsoon during glacials (Masson et al., 2000; Wang et al., 2008). This proposed history is not contradicted by modeling performed by Arpe et al. (2011), who simulated two refuge areas of thermophilous trees during the Last Glacial Maximum, to the north and south of the eastern Anatolia (Fig. 1b), respectively. Extinction of Taxodiaceae can be regarded as being caused by human activities, as *Glyptostrobus pensilis* today suffers in China and Vietnam.

Examination of the present dispersal of ecosystems with *Pterocarya fraxinifolia*, *Zelkova* (*Z. abelicea*, *Z. crenata*, *Z. sicula*), *Liquidambar orientalis* and *Parrotia persica* in the Central and Eastern Mediterranean region and Middle East leads us to foresee their forthcoming re-expansion in Europe within the frame of the warming in progress, maybe through some re-introduction processes in order to counterbalance the expected increase in dryness over the Mediterranean region (Giorgi and Lionello, 2008; Somot et al., 2008).

7. Conclusions

The long continuous pollen record from Site 380, completed by several discontinuous Miocene pollen floras, provides a unique opportunity to synthesize the pattern of plant extinctions along the last 6 Ma in the Anatolian region known by its plant refuges.

Anatolia must be considered as a refuge area for thermophilous-hygrophilous plants since the early Pliocene (at about 5 Ma), scattered in two territories, on its northern and southern coastlines. The onset of this status of thermophilous-hygrophilous plant refuge appears as a consequence of both reinforcement of East Africa monsoon and retreat of the epicontinental Paratethys Sea.

Contraction and division of thermophilous-hygrophilous plant refuges in Europe and around the Mediterranean region in the past 5 Ma is a consequence of physiographic evolution (mountain uplift), climatic changes (repeated severe coolings and aridifications), introduction of Mediterranean seasonality and more recently human activities.

The most striking example is provided by the swampy Taxodiaceae genus *Glyptostrobus*, which might have persisted along the southern Black Sea shore until recently.

Cedrus is documented to be a continuous component of the Anatolian flora since at least 23 Ma.

The present thermophilous-hygrophilous relictual trees in Anatolia, *Pterocarya fraxinifolia*, *Zelkova abelica* and *Liquidambar orientalis*, could benefit from the present climate warming for some re-expansion in Europe.

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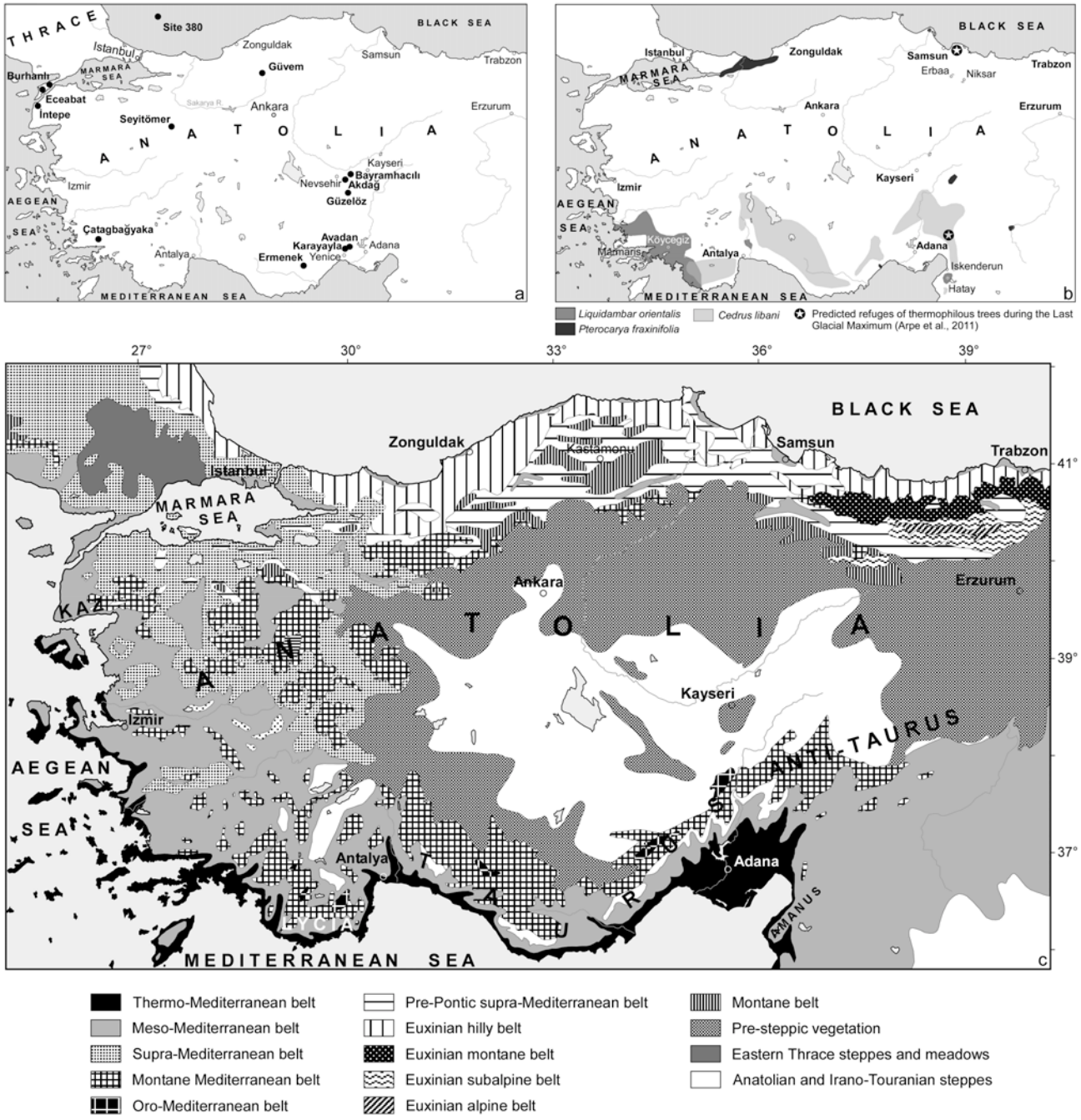


Fig. 1. Location and vegetation maps.
a, Study area and location of pollen sites (black dots);
b, Present-day distribution of *Liquidambar orientalis*, *Pterocarya fraxinifolia* and *Cedrus libani* in Anatolia (from: Quézel and Médail, 2003), compared to the predicted location of

thermophilous trees during the Last Glacial Maximum according to the model T106EH5 developed by Arpe et al. (2011);
c, Simplified present-day vegetation map of Anatolia (from: Quézel and Barbero, 1985).

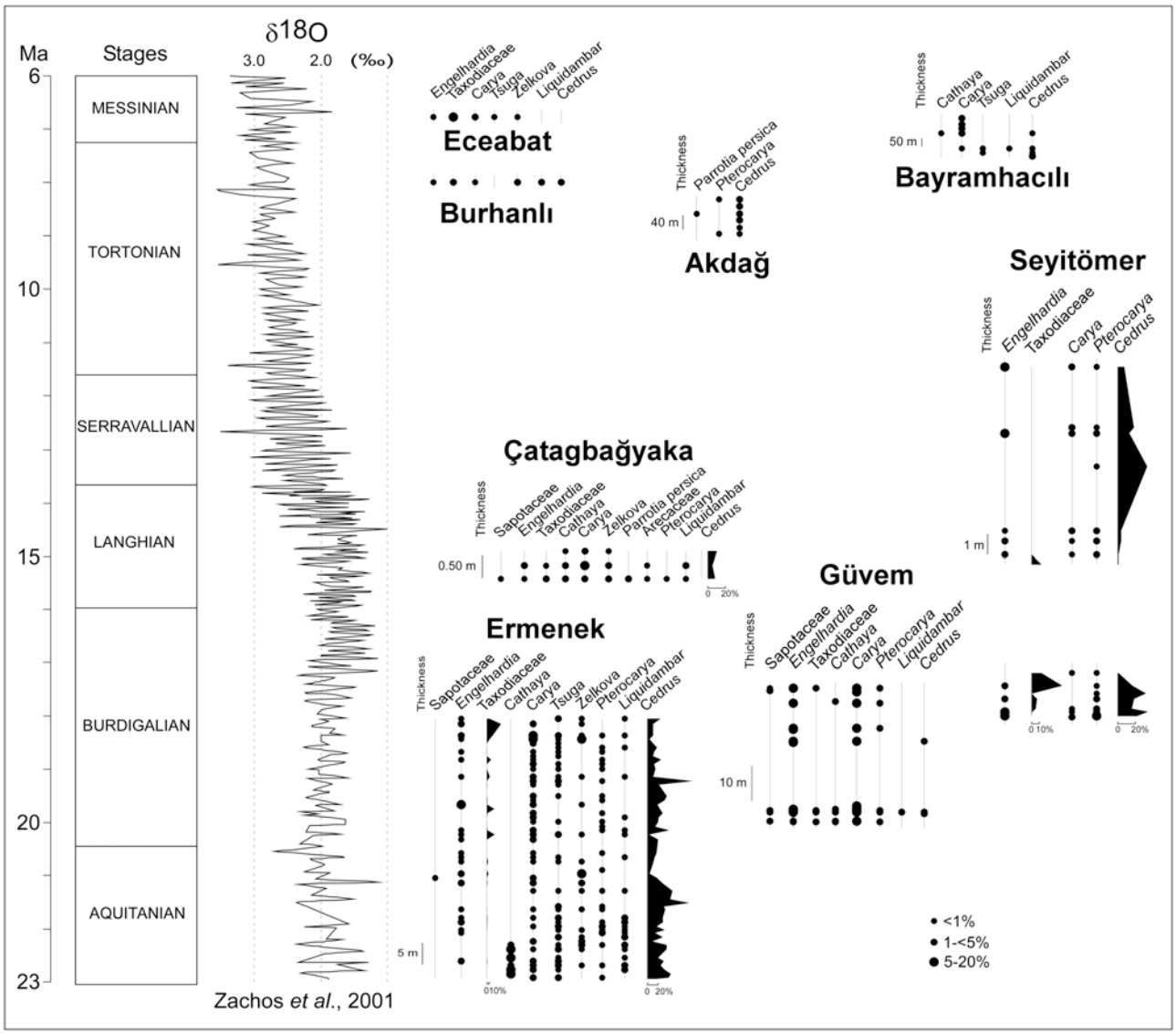


Fig. 2. Selected taxa from Anatolian pollen records chronologically distributed between 23 and 6 Ma. A curve replaces solid dots for Taxodiaceae and *Cedrus* when a continuous record with significant percentage is available. The chronostratigraphic timescale is from Lourens et al. (2005).

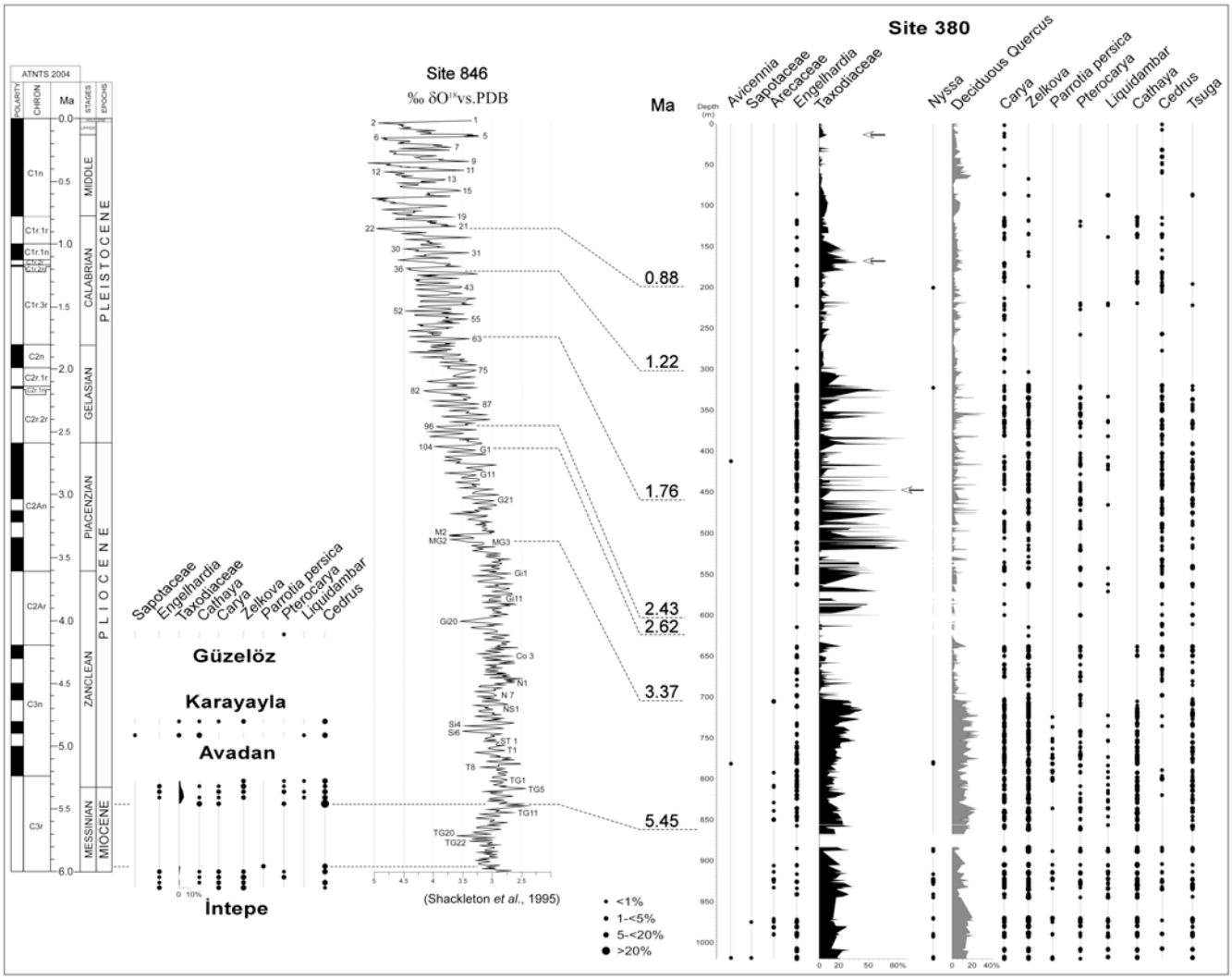
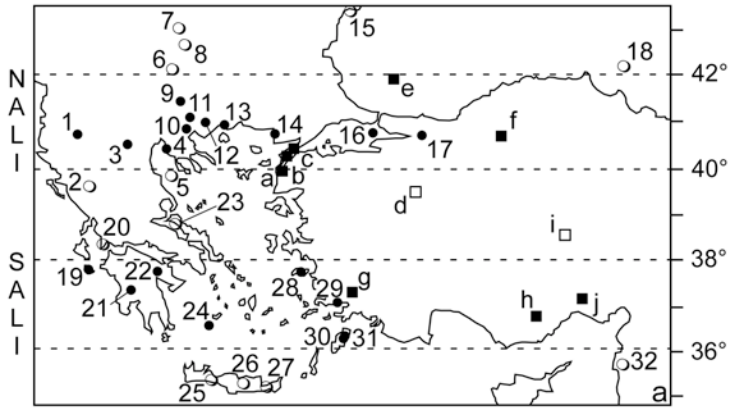
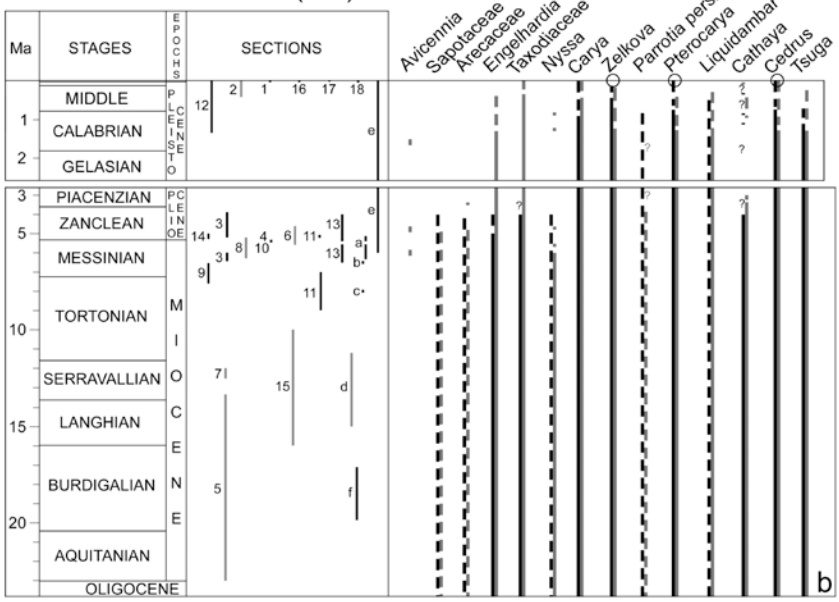


Fig. 3. Selected taxa from Anatolian pollen records chronologically distributed between 6 Ma and Present. A curve is drawn for Taxodiaceae. The major chronostratigraphic relationships between pollen records and the reference oxygen isotope curve are established by Melinte-Dobrinescu *et al*. (2009) for İntepe and Popescu et al. (2010) for Site 380. Arrows indicate the origin of pollen photographs of Taxodiaceae shown in Plate I. The chronostratigraphic timescale is from Lourens et al. (2005). White spaces between continuous records (Taxodiaceae, deciduous *Quercus*) correspond to unrecovered sediment and/or non sampled slump intervals, and detritals such as the Pebly Breccia (874.00–883.50 m).



North latitudinal interval (NLI): 40° - 42°N



South latitudinal interval (SLI): 36° - 38°N

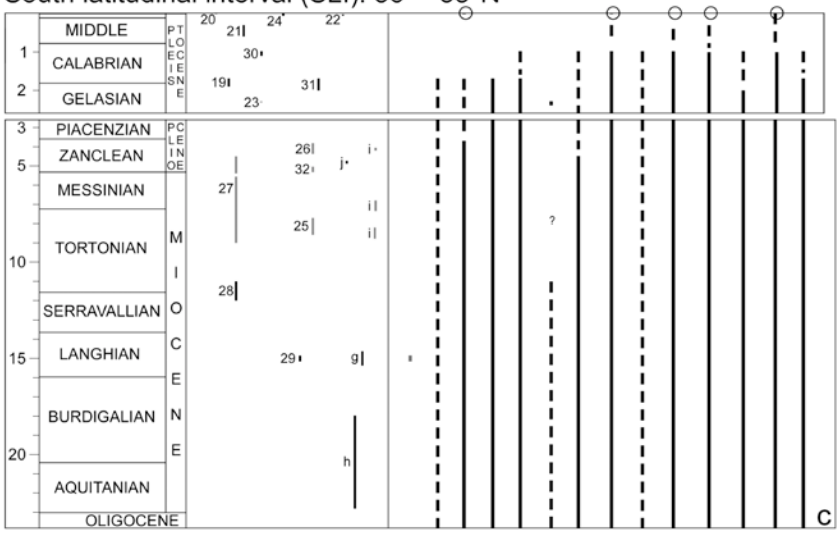


Fig. 4. Compared geographic and chronological distribution of some taxa within the latitudinal range of Anatolia (*ca*. 36° to *ca*. 42° North) for the last 23 Ma.
a, Location map of the selected pollen floras (for names, associated numbers and references: see Table 1). Black dots: compared pollen floras located within the two latitudinal intervals 40–42°N (North Anatolia latitudinal interval: NALI) and 36–38°N (South Anatolia latitudinal interval: SALI); circles: compared pollen floras located out of these latitudinal intervals; black squares: new pollen floras presented in this work located within these latitudinal intervals (a, İntepe; b, Eceabat; c, Burhamlı; e, Site 380; f, Güvem; g, Çatakbağyaka; h, Ermenek; j, Avadan and Karayayla); blank squares: new pollen floras presented in this work located out of these latitudinal intervals (d, Seyitömer; i, Bayramhacılı, Akdağ, and Güzelöz).
b and c, Chronological location of pollen floras (in light grey, localities out of the concerned latitudinal interval) and chronological extension of some taxa within (and close to) the latitudinal interval 40°–42°N (NALI) and 36°–38°N (SALI), respectively. The chronological scale is doubled for the time-interval 0–2.6 Ma. Continuous vertical lines indicate constant records attested by significant amount of pollen grains; discontinuous vertical lines indicate intermittent records characterized by low amount of pollen grains. Circles at present time point out elements still living in Anatolia.
b, NALI: 40°–42°N. Thanks to the new pollen data presented in this paper, the history of taxa can be reconstructed for the last 23 Ma and in detail for the last 6 Ma, expressed by the vertical (continuous or discontinuous) dark grey lines. The black vertical lines synthesize the pre-existing pollen data at the scale of the considered latitudinal interval.
c, SALI: 36°–38°N. Only black vertical lines synthesize all the available pollen data at the scale of the considered latitudinal interval.

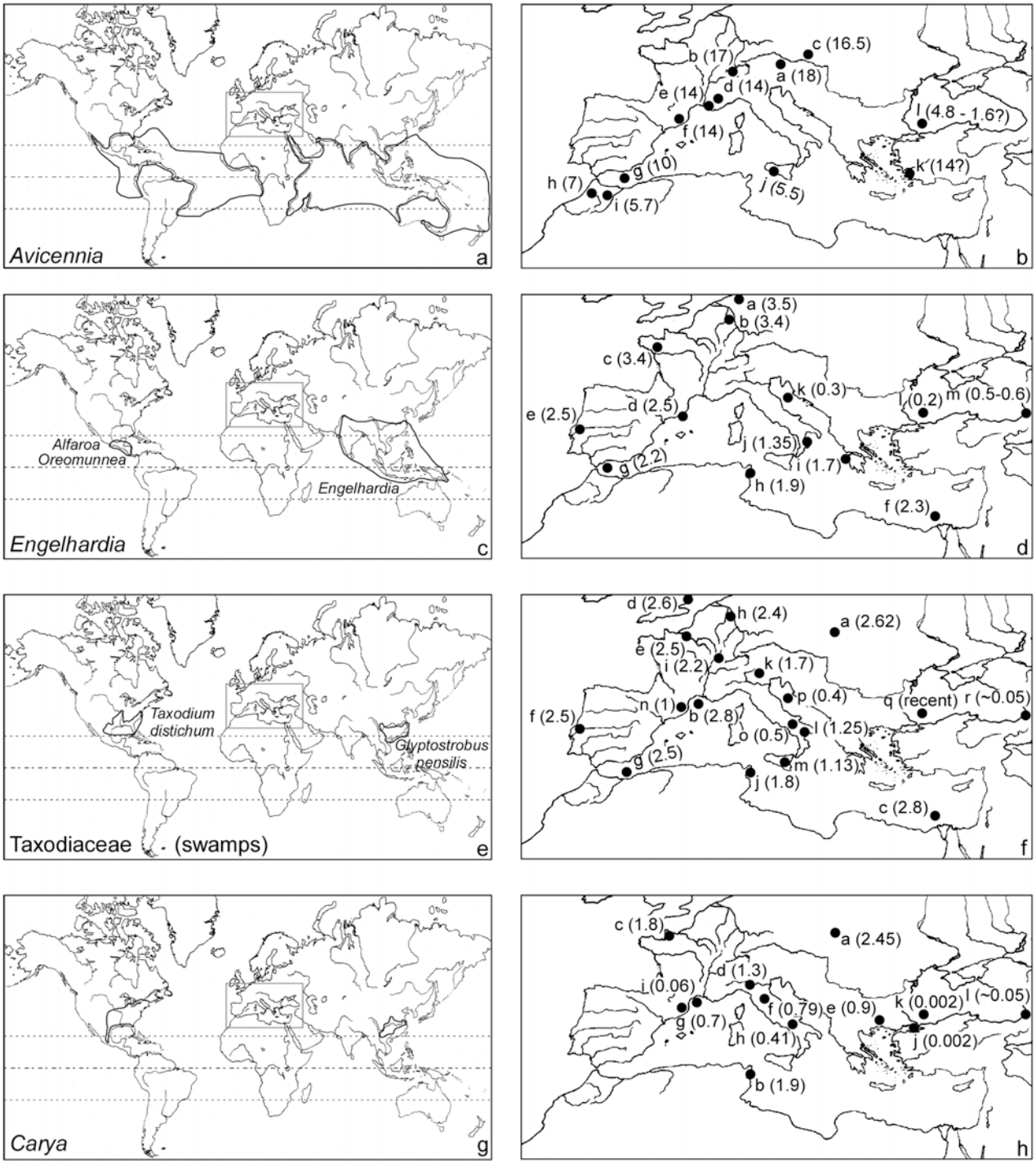


Fig. 5. Present-day distribution maps of four reference taxa (a, *Avicennia*; c, *Engelhardia*; e, Taxodiaceae inhabiting swamps; g, *Carya*) and their last pollen record (ranked by decreasing

age, indicated in brackets after the locality reference letter) in Europe (b, *Avicennia*; d, *Engelhardia*; f, Taxodiaceae inhabiting swamps; h, *Carya*), North Africa and Near East (see Table 2 for list of localities and relevant literature).

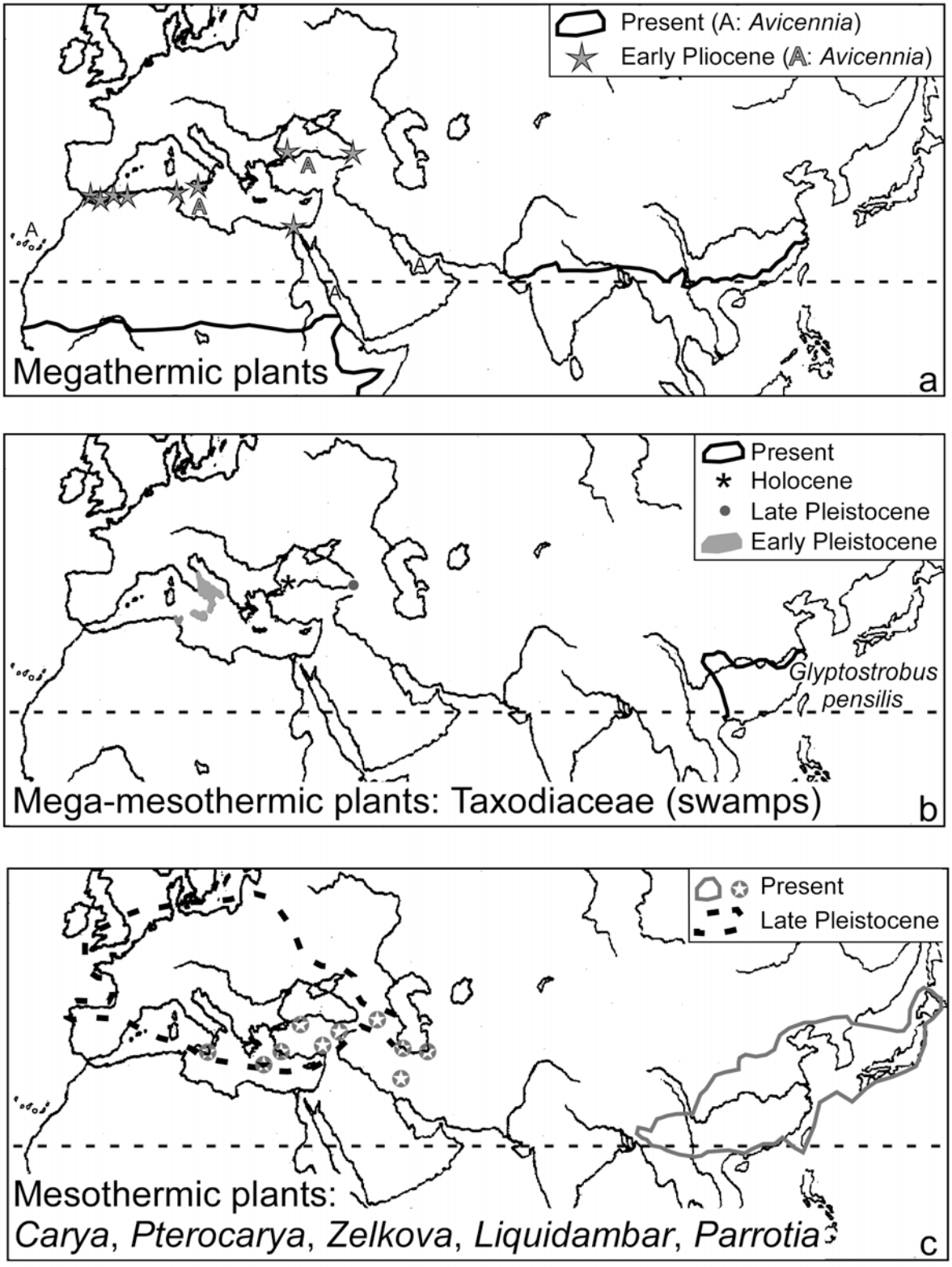


Fig. 6. Proposed past refuge areas compared to present distribution of some thermophilous taxa or groups of taxa in Eurasia.
a, Megathermic elements;
b, Taxodiaceae (swamp elements);
c, Mesothermic elements (*Carya*, *Pterocarya*, *Zelkova*, *Liquidambar*, *Parrotia*).

N°	Localities	References
1	Maliq	Denèfle et al. (2000)
2	Ioannina	Tzedakis (1993, 1994)
3	Ptolemais	Ioakim (1984) Klosterboer-van Hoeve (2000) Biltekin (2010)
4	Trilophos	Biltekin (2010)
5	Nireas 1	Drivaliari (1993) Jiménez-Moreno et al. (2007)
6	Ravno Pole	Drivaliari (1993) Jiménez-Moreno et al. (2007)
7	Ruzhintsi	Jiménez-Moreno (2005) Jiménez-Moreno et al. (2007)
8	Beli Breg	Ivanov et al. (2007)
9	Sandanski	Ivanov (2003) Jiménez-Moreno et al. (2007)
10	Lion of Amphipoli	Suc (unpublished)
11	Serres	Karistineos & Ioakim (1989) Suc (unpublished)
12	Tenaghi Philippon	Wijmstra (1969) Wijmstra & Smit (1976) Van der Wiel & Wijmstra (1987a, b) Tzedakis et al. (2006)
13	Nestos 2	Drivaliari (1993) Jiménez-Moreno et al. (2007)
14	Enez	Melinte-Dobrinescu et al. (2009) Biltekin (2010)
15	Balchik C136A	Ivanov et al. (2007)
16	MAR98-9	Mudie et al. (2002)
17	Lake Sapanca	Leroy et al. (2009, 2010)
18	Black sea B7	Mudie et al. (2002)
19	Zakynthos Citadel	Suballyova (1997) Subally et al. (1999)
20	Acheloos Delta (holes OEN 1 & 2)	Fouache et al. (2005)
21	Megalopolis	Okuda et al. (2002)
22	Core A11	Urban & Fuchs (2005)
23	Zeli	Ioakim & Rondoyani (1988)
24	Core C69	Geraga et al. (2005)
25	Makrilia	Sachse et al. (1999)
26	Aghios Vlassios	Drivaliari (1993) Jiménez-Moreno et al. (2007)
27	Sitia	Ioakim et al. (1997)
28	Mavradzei	Ioakim & Solounias (1985)
29	Kultak – Muğla – Milas	Kayseri-Özer (2014)
30	Tsampika	Joannin et al. (2007)
31	Cape Vagia	Buisine (2000) Cornée et al. (2006)
32	Lattaquie	Jiménez-Moreno et al. (2007)

Table 1. Pollen localities considered for comparison with the present-work pollen floras. Numbers refer to Figure 4.

N°	Regions	Localities	References
Avicennia	Present distribution		Tomlinson (1986)
A	Central Europe	Strass-Eberschwang	Jiménez-Moreno et al. (2008)
B	Central Europe	Häutlingen	Jiménez-Moreno (2005)
C	Central Europe	Göllersdorf	Jiménez-Moreno et al. (2008)
D	Southeastern France	Châteauredon	Besson et al. (2005)
E		Bayanne	Besson et al. (2005)
F	Catalonia	La Rierussa	Bessedik (1985) Jiménez-Moreno (2005)
G	Alboran Sea	Andalucia A1	Jiménez-Moreno (2005) Jiménez-Moreno et al. (2010)
H	Southern Rif	NRT2	Bachiri Taoufiq (2000) Bachiri Taoufiq et al. (2000)
I	Southern Rif	Col de Touahar	Bachiri Taoufiq (2000) Bachiri Taoufiq et al. (2000)
J	Sicily	Eraclea Minoa	Suc and Bessais (1990) Fauquette et al. (2006)
K	Southwest Turkey	Kultak – Muğla – Milas	Kayseri-Özer (2014)
L	Black Sea	Site 380	Popescu et al. (2010) Biltekin (2010)
Engelhardia	Present distribution		Aubréville (1974) An-Ming (1982)
A	Hanover	Oldenswort 9	Menke (1975)
B	The Netherlands	Koningsbosch	Zagwijn (1960)
C	Brittany	Saint-Jean la Poterie	Fourniguet et al. (1989)
D	Catalonia	Garraf 1	Suc and Cravatte (1982)
E	Portugal	Rio Maior F58 and F16	Diniz (1984)
F	Offshore Nile Delta	NAF 2	Drivaliari (1993)
G	Alboran Sea	Andalucia G1	Feddi et al. (2011)
H	Gulf of Hammamet	Jiriba 1	Mriqo (2010)
I	Zakynthos Island	Citadel	Suballyova (1997)
J	Calabria	Vrica C	Combourieu-Nebout (1990)
K	North Adriatic Sea	Bonaccia 1, Bonaccia Sud 1, Esmeralda 1	Suc (1982a, b, c)
L	Black Sea	Site 380	This paper
M	Black Sea	West Georgia	Shatilova et al. (2011)
Taxodiaceae (swamps)	Present distribution		Sternitzke (1972) Fang et al. (2011)
A	Poland	Wólka Ligezowska	Winter *in* Popescu et al. (2010)
B	Gulf of Lions	Autan 1	Cravatte and Suc (1981) Suc et al. (1992)
C	Offshore Nile Delta	NAF 2	Drivaliari, 1993
D	East Anglia	Several localities	Gibbard et al. (1991)
E	Normandy	La Londe K	Clet-Pellerin et al. (1999)
F	Portugal	Rio Maior F58 and F16	Diniz (1984)
G	Alboran Sea	Nador 1	Feddi et al. (2011)
H	The Netherlands	Meinweg	Zagwijn (1960)

J	Gulf of Hammamet	Jiriba 1	Mriqo (2010)
K	Po Valley	Leffe	Ravazzi and Moscariello (1998)
L	Calabria	Montalbano Jonico	Joannin et al. (2008)
M	Sicily	Caltagirone	Dubois (2001)
N	Catalonia	Cal Guardiola	Postigo Mijarra et al. (2007)
O	Campania	Vallo di Diano	Russo Ermolli (1994)
P	North Adriatic Sea	Bonaccia 1, Bonaccia Sud 1	Suc (1982a, b)
Q	Black Sea	Site 380	This paper
R	Black Sea	West Georgia	Shatilova et al. (2011)
Carya	Present distribution		An-Ming (1982) Thompson et al. (2000)
A	Poland	Wólka Liezawska	Winter *in* Popescu et al. (2010)
B	Gulf of Hammamet	Jiriba 1	Mriqo (2010)
C	Normandy	Bosq d'Aubigny	Clet-Pellerin (1983) Clet-Pellerin et al. (1985)
D	Po Valley	Stirone	Bertini (2001)
E	Northen Greece	Tenaghi Philippon	Van der Wiel and Wijmstra (1987b)
F	Central Italy	Valdarno	Albianelli et al. (1995)
G	Catalonia	Bòbila Ordis	Julià Bruguès and Suc (1980) Suc et al. (1992) Leroy (2008)
H	Calabria	Vallo di Diano	Russo Ermolli (1994) Russo Ermolli et al. (2010)
I	Gulf of Lions	PRGL1-4	Suc et al. (in progress)
J	Marmara Sea	MAR 98-9	Mudie et al. (2002)
K	Black Sea	Site 380	This paper
L	Black Sea	West Georgia	Shatilova et al. (2011)

Table 2. References for present-day distribution of *Avicennia*, *Engelhardia*, Taxodiaceae swamps, and *Carya*. Pollen localities considered for comparison. Letters refer to Figure 5.

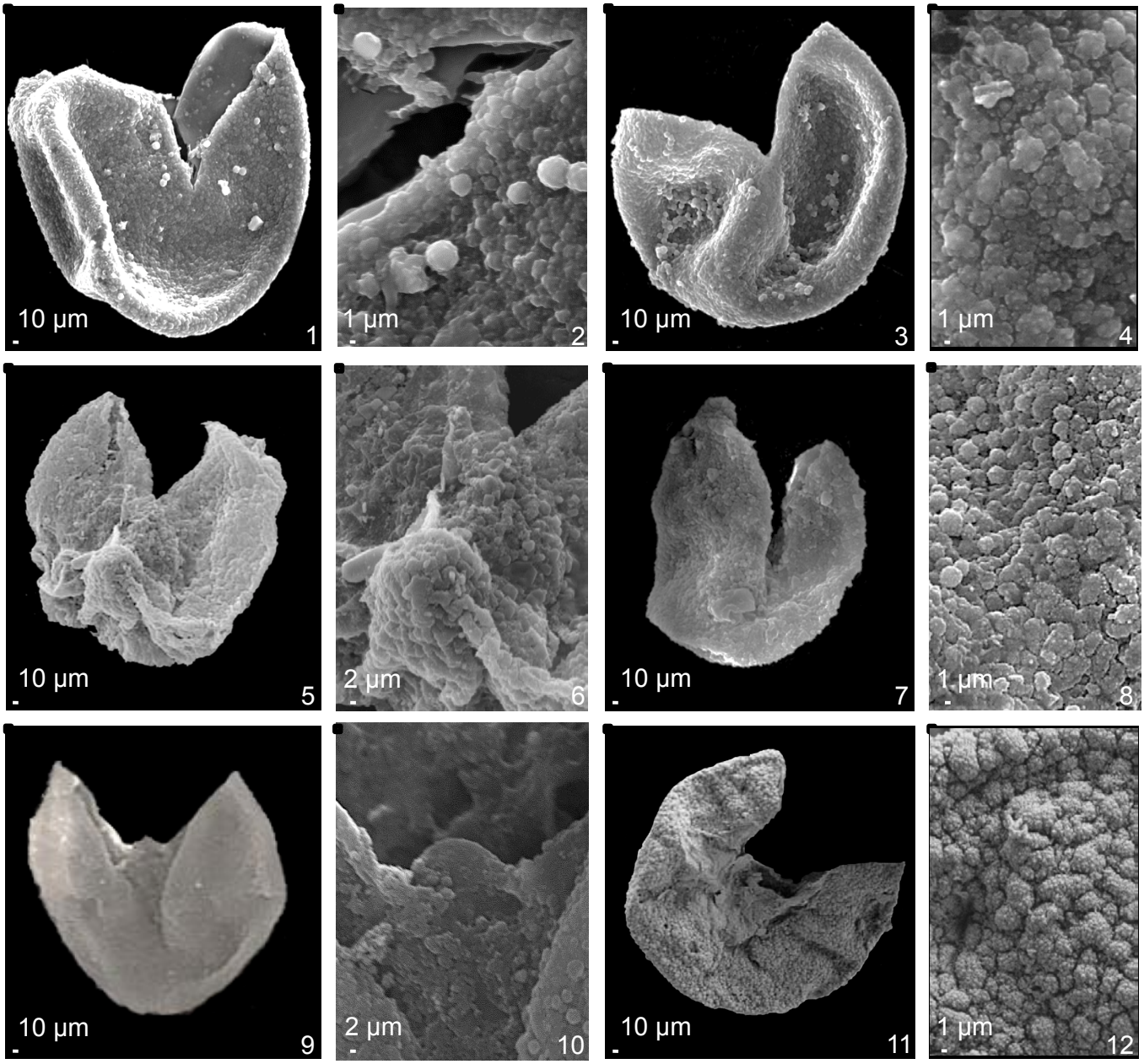


Plate I. Present and fossil pollen grains of Taxodiaceae.
1 to 4, Two modern pollen grains of *Glyptostrobus pensilis* (Staunton ex D. Don) K. Koch, originating from China (Herbarium of the Sun Yat-sen University, Guangzhou; sample number: 28781; originating from the Herbarium of the Lingnam University, China): 1, General view (x2000); 2, Detail of the sculpture (x12000); 3, General view of another grain (x2000); 4, Detail of its sculpture (x12000).
5 and 6, Pollen grain from Site 380 (448 m depth, lower Pleistocene): 5, General view showing the papilla (x2000); 6, Detail of the sculpture in the papilla area (x6000).

7 and 8, Pollen grain from Site 380 (448 m depth, lower Pleistocene): 7, General view (x2000); 8, Detail of the sculpture (x12000).
9 and 10, Pollen grain from Site 380 (168 m depth, Middle Pleistocene): 9, General view showing the papilla (x2000); 10, Detail of the sculpture in the papilla area (x6000).
11 and 12, Pollen grain from Site 380 (13.50 m depth, Holocene): 11, General view (x2000); 12, Detail

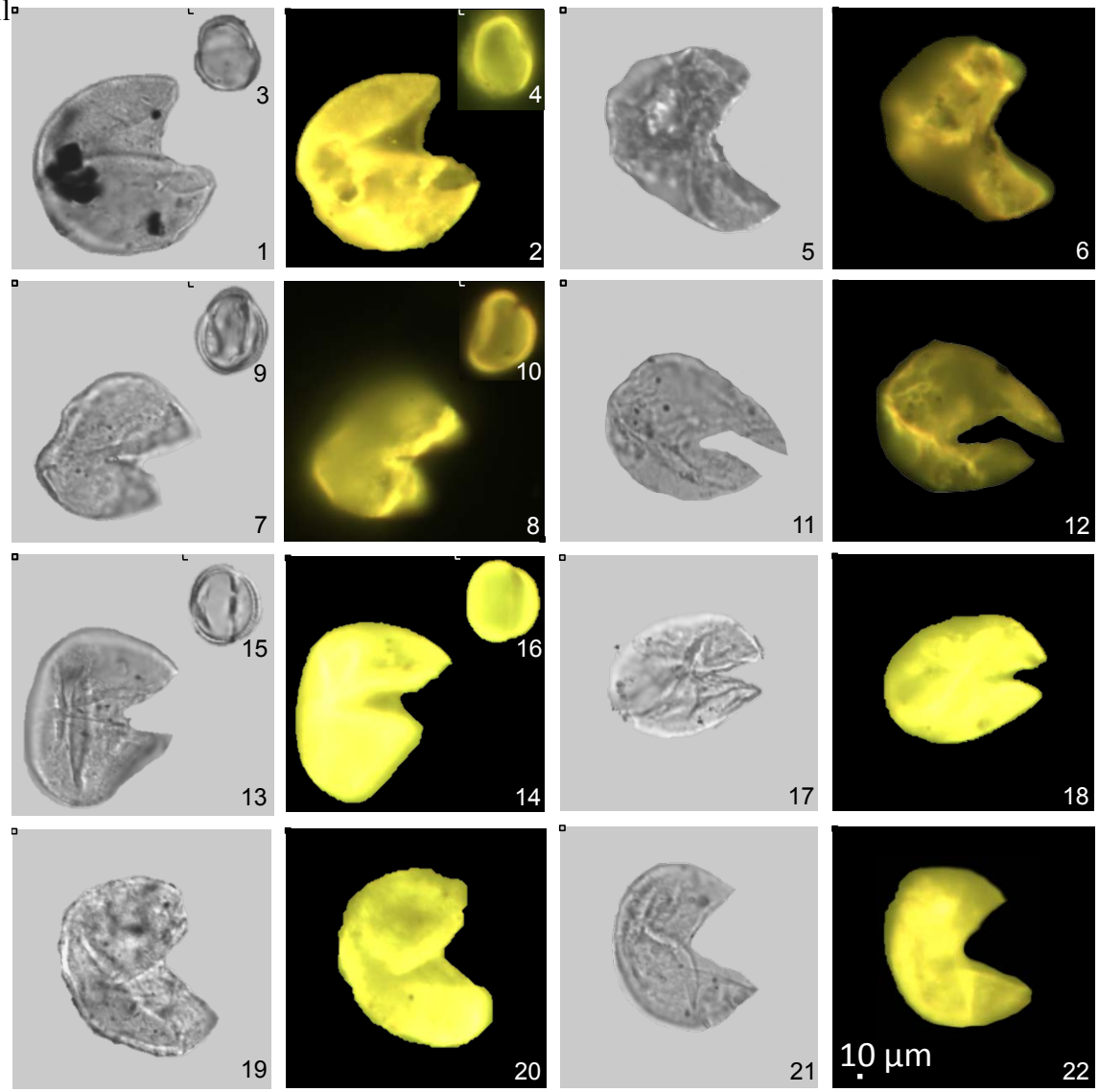


Plate II. Comparative examination of some Taxodiaceae and *Artemisia* fossil pollen grains in light and fluorescence microscopy. Scale-bar = 10 µm for all the views.
1–8, at 2 m depth: 1, Taxodiaceae in light microscopy; 2, Same Taxodiaceae pollen in fluorescence microscopy; 3, *Artemisia* in light microscopy; 4, Same *Artemisia* pollen in fluorescence microscopy; 5, Taxodiaceae reworked pollen in light microscopy; 6, Same Taxodiaceae reworked pollen in fluorescence microscopy.
7–10, at 30.51 m depth: 7, Taxodiaceae in light microscopy; 8, Same Taxodiaceae pollen in fluorescence microscopy; 9, *Artemisia* in light microscopy; 10, Same *Artemisia* pollen in fluorescence microscopy.
11–12, at 49.47 m depth: 11, Taxodiaceae reworked pollen in light microscopy; 12, Same Taxodiaceae reworked pollen in fluorescence microscopy.
13–18, at 169.16 m depth: 13, Taxodiaceae in light microscopy; 14, Same Taxodiaceae pollen in fluorescence microscopy; 15, *Artemisia* in light microscopy; 16, Same *Artemisia* pollen in

fluorescence microscopy; 17, Taxodiaceae in light microscopy; 18, Same Taxodiaceae pollen in fluorescence microscopy.
19–20, at 334.50 m depth: 19, Taxodiaceae in light microscopy; 20, Same Taxodiaceae pollen in fluorescence microscopy.
21–22, at 976.00 m depth: 21, Taxodiaceae in light microscopy; 22, Same Taxodiaceae pollen in fluorescer

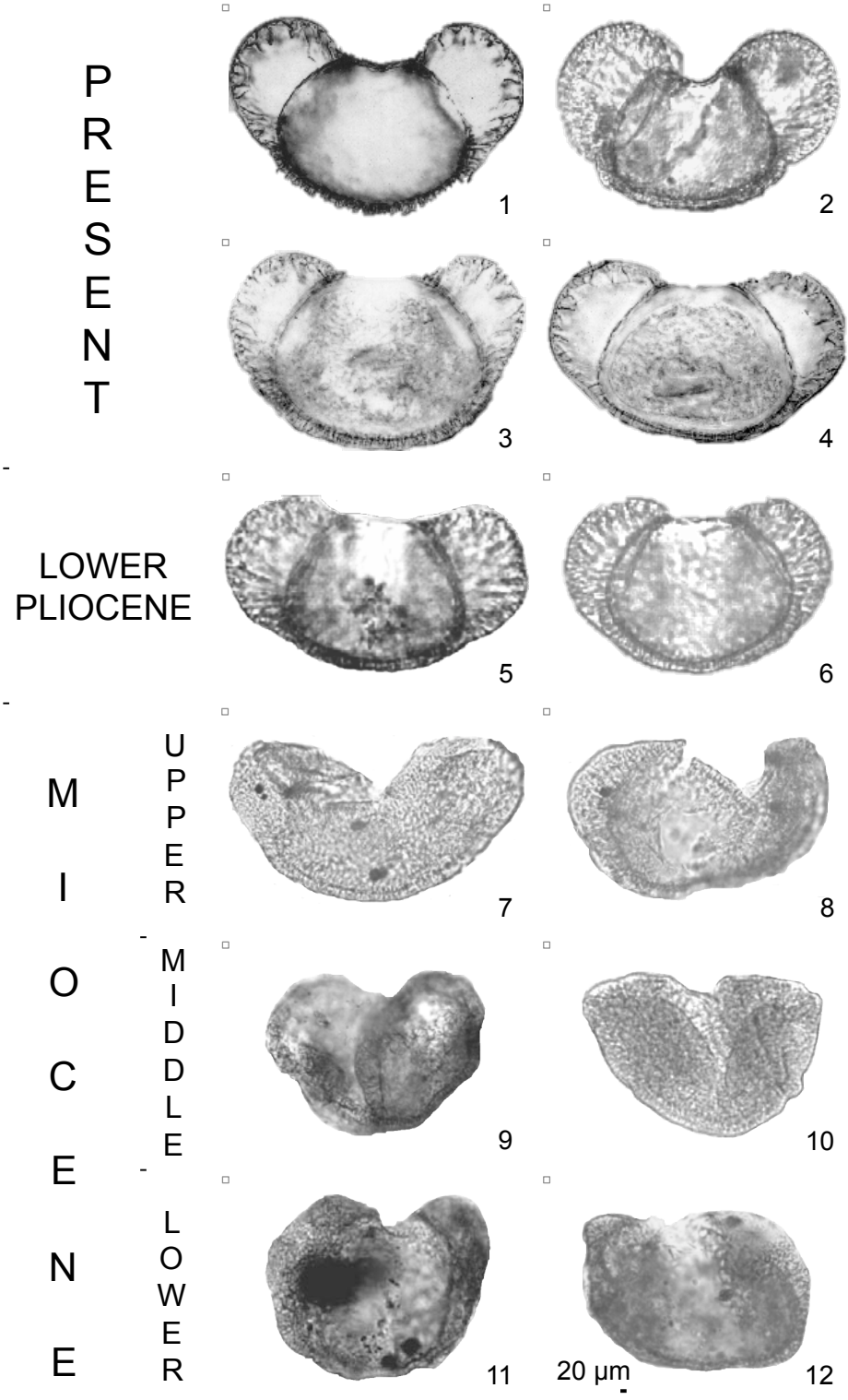


Plate III. Photographs of present and fossil pollen grains of *Cedrus* in profile view.

1-4, Pollen grains of the four living species: 1, *C. libani* A. Rich.; 2, *C. brevifolia* (Hook. f.) Henry; 3, *C. deodara* (Roxb.) G. Don.; 4, *C. atlantica* (Endl.) Manetti. ex Carrière. Photographs have been taken by one of us (J.-P.S.) from pollen slides of the ISEM collection (Montpellier) corresponding to plant samples indicated by Aytuğ (1961).
5-12, Fossil pollen grains from several localities: 5-6, Site 380 (Zanclean); 7-8, İntepe (latest Messinian); 9, Çatakbağyaka (middle Miocene); 10, Seyitömer (middle Miocene); 11-12, Ermenek (Aquitanian).
The scale-bar, shown in picture 12, is the same for all the views.